

Five theoretical excursions into evolutionary
ecology: on coevolution, pheromone
communication, clutch size
and bird migration



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FIVE THEORETICAL EXCURSIONS INTO EVOLUTIONARY ECOLOGY:
ON COEVOLUTION, PHEROMONE COMMUNICATION,
CLUTCH SIZE AND BIRD MIGRATION

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ABSTRACT

The thesis addresses four different significant problems in evolutionary ecology. These are analyzed theoretically by means of mathematical methods. (1) Fisher's fundamental theorem is extended to the case of coevolution between competing predators. It is shown that character convergence is impossible in models for coevolution between competing predators, owing to the constraint imposed by the dynamics of the resources. (2) A theory is developed for the impact of a pheromone communication system on the population dynamics of the moth species adopting it. It is shown that the sexual communication system might have a regulatory effect if litter size and the males ability to discriminate between different levels of concentrations is not too large. The evolution of pheromones is discussed from the point of view of the model. (3) A theory for the evolution of clutch size is developed, showing that compensatory egg laying and clutch size reduction owing to, respectively, high incidencies of unhatched eggs and predation. The problem of how reproductive success varies between and within species is discussed. (4) The stability of bird migration patterns is investigated. It is shown that asymmetric competition both at breeding and wintering sites is essential for leap frog migration to arise, whereas migration costs are sufficient for generating a chain migration pattern. Stable migratory divides may arise owing to both competition and migration costs.

LIST OF PAPERS

- i. Lundberg, S. & N.C. Stenseth, 1985. Coevolution of competing species: Ecological character displacement.
- Theor. Pop. Biol. 27: 105-119.
- ii. Lundberg, S. & C. Löfstedt. Intraspecific competition in the sex communication channel: A selective force in the evolution of moth pheromones (MS)
- iii. Lundberg, S. 1985. The importance of egg hatchability and nest predation in clutch size evolution in altricial birds. - Oikos 45: 110-117.
- iv. Lundberg, S. On reproductive success, its evolutionary regulation and variation within and between species.
- Oikos (accepted).
- v. Lundberg, S. & Alerstam, T. Bird migration patterns: Conditions for stable population segregation (MS)

Coevolution (Paper i)

The starting point for this venture was a model proposed by MacArthur & Levins (1964), which has been reanalysed by Lawlor & Maynard Smith (1976). It includes two very simple-minded predators with linear functional response and two resource species with logistic renewal dynamics.

MacArthur & Levins (op. cit.) used the fitness set concept (Levins 1968). They assumed that there is a kind of constraint such that organisms able to utilize one resource very efficiently, will necessarily be less efficient in their use of the other. The utilization of the two resources defines an animal's strategy, which may then be visualized as a point in the first quadrant of a coordinate system (put, say, the utilization of resource one on the abscissa and the utilization of resource two on the ordinate). MacArthur's & Levins' constraint can be drawn as a curve in the coordinate system, connecting the specialist strategies situated on the axes (Fig. 1). Strategies on and below the constraint curve define the set of biologically feasible strategies. The optimal strategy will usually lie on the constraint curve, as the longer away from the origin a strategy is situated, the more can a creature adopting it eat.

The difference between MacArthur's & Levins' original treatment and Lawlor's & Maynard Smith's (op.cit.) is twofold. First, the latter authors used separate fitness sets for the two consumer species. Secondly, they used a much more elaborate optimization method, as they applied the concept of evolutionarily stable strategies (ESS), see Maynard Smith (1982).

In our treatment (paper i), we went a step further and specified a genetic system (the conventional, one locus two alleles system) and reanalysed the model again, using quantitative genetics. Each species' three phenotypes could then be put into a coordinate system. We defined the mean strategy as the point in the coordinate system, which for a given gene frequency, corresponds to the average individual in the population. The mean strategy curve connects the mean strategies obtained by varying the gene frequency. This curve is at least formally analogous to the constraint curves used in the earlier treatments. By assuming that two species have the same constraint curve, one also assumes that the two species have exactly the same range of possible phenotypes. That is, they are basically not two species but one. We analysed these mean strategy curves further and were able to demonstrate the connections between quantitative

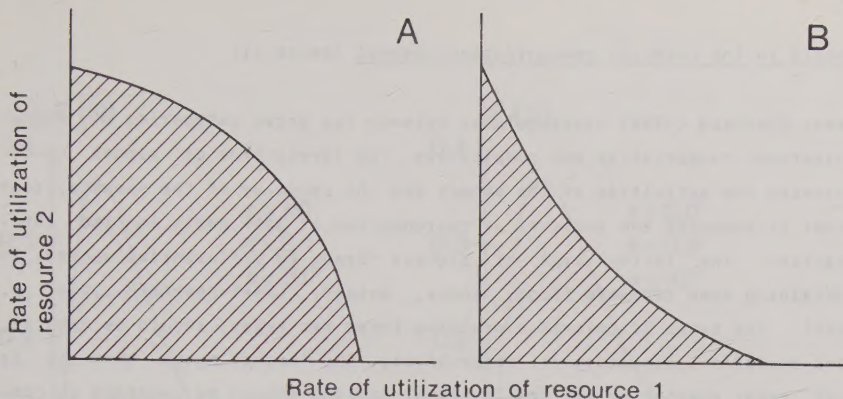


Figure 1. Constraints of the kind used by MacArthur & Levins (1964) and Lawlor & Maynard Smith (1976). (A) When the constraint curve is convex (from above) the optimum strategy usually is to include both resources in the diet. This occurs if the resources are fairly similar, such that no special adaptations are needed for utilizing either of them. (B) A concave constraint curve is thought to arise when the difference between resources is so large that special adaptations are needed for the utilization of each of them. This will in general lead to specialization.

genetics and the kind of optimization models used by Lawlor & Maynard Smith.

In addition to this more technical discussion, we also wanted to investigate the robustness of Lawlor's & Maynard Smith's conclusion that character divergence is the only possible outcome of the coevolution of competing predators. It was indeed robust, and it is obvious why. Consider what kind of a situation that would lead to character convergence in the model. Then, each consumer must be more specialized under allopatry than under sympatry. This is indeed counterintuitive. In addition the model shows that such a situation cannot arise, since the mean strategy evolved under sympatry constitutes the utmost degree of specialization that can be stable under allopatry. A consumer which is more specialized than that, would drive its main resource to extinction. However, if such specialized strategies could exist under allopatry, then the model shows that they would in fact be unable to coexist.

The significance of this result is appreciated if the model is compared with models without resource dynamics. Over-exploitation of a rigid gaussian bell jar type of spectrum of inanimate resources is of course impossible. In such models convergence becomes a possibility, but not owing to competition but as a result of the selection pressure exerted by the resource spectrum itself (c.f., Slatkin 1980).

West-Eberhard (1984) distinguishes between two broad categories of communication: co-operative and competitive. The former type of signal co-ordinates the activities of the sender and the receiver of the message, such that it enhances the survival or reproduction of both parts in the interaction. The latter type of signals "leads to differential success in obtaining some resource (food, space, mate)". (West-Eberhard 1984, p. 284). The types of selection moulding these two types, should be natural, and social/sexual selection; respectively. She further notes that it is not clear whether or not female sexual calling should be regarded as competitive. In paper ii a scenario is described for how female calling contests may take place as a consequence of properties inherent in pheromone communication systems. First I summarize the background in three points:

(i) There is an enormous variation in production and release rate of pheromones within species (Haynes et al. 1984). The same is true for male sensitivity to the pheromones. (Linn et al. 1984). This variation in production may be the cause of the large variation in captures between traps in field studies, where living females are used as baits; in fact it has been shown that such "attractive" females ("superfemales") are effective baits irrespective of their position in a trap grid (Löfstedt, pers.comm.). That is, their propensity to attract males is caused by some intrinsic factors, rather than local topographical and meteorological ones.

(ii) Moths produce their odours in minute quantities. Thus A. segetum releases a few nanograms (i.e., 10^{-9} g) of (Z)-7-dodecenylacetate (Löfstedt, pers.comm.) whereas Trichoplusia ni releases the same compound, but at the herculean microgram level (Bjostad et al. 1984). There are no biochemical or physiological reasons known today for such a large inter-specific variation. A tentative conclusion is that as far as the function of a pheromone is concerned the level of its production is of minor importance.

(iii) Disruption of pheromone communication is used in pest control; the environment is saturated with pheromones, which leads a reduced mating success (Shorey 1977). Three explanations have been proposed for the phenomenon (Shorey 1977): sensory adaptation, central nervous system (CNS) habituation, and "confusion". Sensory adaptation and (CNS) habituation are essentially the same type of mechanisms, the former is a masking of stimuli at the receptor level, whereas the latter occur within the CNS. "Confusion" is the effect of competition between artificial pheromone sources and females.

Wall & Perry (1978, 1980) made observations that might throw light on the mechanism behind confusion. They used traps organized in a row in the wind direction, and baited with an artificial pheromone. They found clear position effects, such that the most upwind trap caught most males. This has now been studied here in Lund in wind tunnel experiments. Although

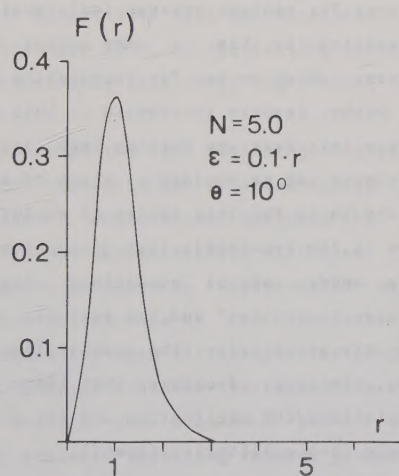
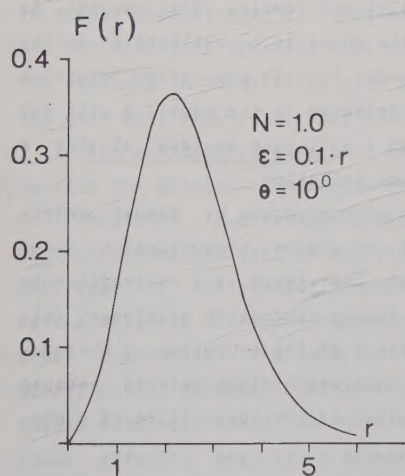
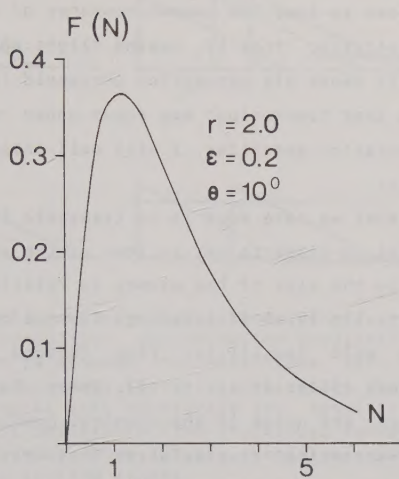
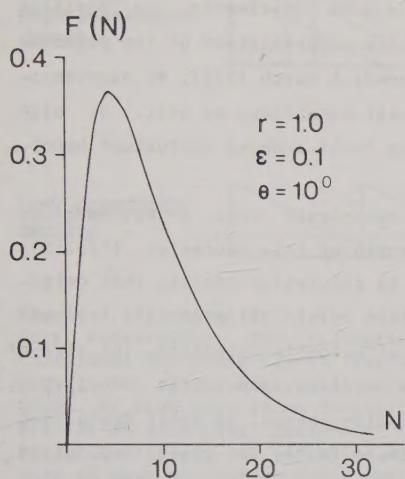


Figure 2. F is the probability that contact is established between a given female and a male N is the density of females and r is the length of the plumes (which are assumed to be circle sectors with the angle $2\theta^0$). The parameter ϵ is explained and discussed in paper ii). Top row: The dependence of the probability for contact on female density for two sizes of plumes. For each size there is a density which gives least noise in the communication. By making the plumes two times larger, this density decreases from five to one female per unit area. Bottom row: The same effect illustrated by varying r for two population densities.

just a pilot study, it reveals the same pattern (see paper ii). The explanation is that the normal response of a male to pheromones, is positive anemotaxis, that is, upwind flight when the concentration of the pheromone is above his perception threshold (Kennedy & Marsh 1974). We hypothesized that "confusion" may occur under natural conditions as well, at high population densities. I will call this the "self-induced confusion" hypothesis.

What we have done is to translate the hypothesis into a mathematical model in order to get an idea of the strength of this mechanism. (Fig. 2). It is the size of the plumes in relation to population density that determines the level of crowding. Given a certain level of pheromone release and male sensitivity [the factors that probably determine the size of plumes (Sower et al. 1971)], there is a certain population density at which the noise in the chemical communication channel is least disturbing for the moths' love affairs. Similarly, there is for a given population density a certain level of production/sensitivity that gives the best chances for contact between individual males and females. What happens is visualized in Fig. 3. The output of the model is an estimate of mating success, which we use for formulating a model for the population dynamics of moths. Readers interested in this is referred to the paper, I will not pursue this task any further here. Instead I will give an idea of how a pheromone can be moulded by means of sexual selection.

The basis for this theory of evolution of pheromones by sexual selection is the hypothesis that disruption of pheromone communication occur also under natural conditions. Further, that there is a correspondence between "confusion" and the evolution of female production / release rate and male sensitivity (the quantitative aspect of the evolution of pheromones). Similarly, I propose that there is a correspondence between sensory adaptations/CNS habituation and the evolution of the composition of a pheromone (the qualitative aspect).

Moths are dependent on olfactory cues, and must have some kind of "olfactory image" of their near surroundings. It seems plausible that they have special adaptations ensuring that the "resolution" of this image is high.

1. The quantitative aspect. Females with pheromone production higher than the average are probably selected for. This is especially true at low densities. At high densities the advantage may be nil or just slight.

How males respond to this increase in pheromone production over evolutionary time depend on the demography of the species. We hypothesize that

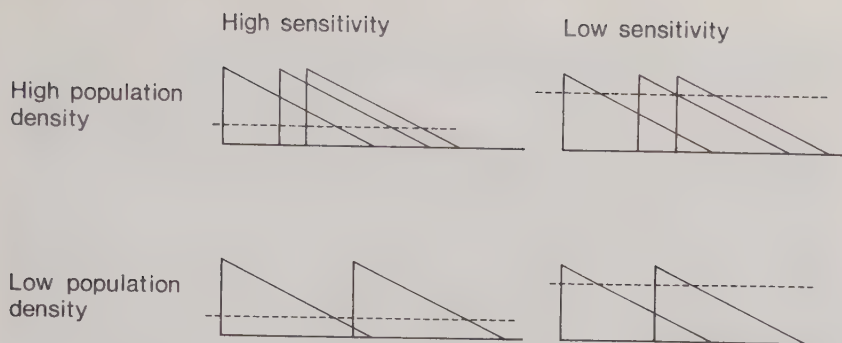


Figure 3. Illustration of the interaction between population density and male sensitivity. The triangles symbolizes concentration gradients in individual pheromone plumes (the wind is assumed to blow from left to right). The dashed horizontal lines represents the males perception thresholds. At high population densities males with relatively low sensitivity are at an advantage, because of their ability to find individual females. At low densities, the situation is reverse. Then highly sensitive males have an edge because of their ability to find plumes.

in stable populations, the variance in sensitivity will be relatively low, and its mean will decrease over evolutionary time. In fluctuating species, the variance in sensitivity will be maintained relatively high level and its mean will stay relatively constant.

2. The qualitative aspect. I mentioned at the very beginning of this section the possible connection between the variation in attractivity and the variation in pheromone production in female moths. However, the "superfemales" may as well be qualitatively as quantitatively different from the rest of the females. The pheromone produced by "superfemales" might have a slightly different composition, for instance by the inclusion of trace components. The ability to perceive such differences, be it just minor, purely phenotypic differences, clearly enhances the resolution of a male's olfactory image. We therefore predict the existence of a "rare odour effect", that is, a selection pressure favouring females producing rare pheromone varieties. These varieties must not be too different, though. Males probably compare the perceived odours with a "template", defining limits to the range of blends releasing the upwind flight behaviour.

One explanation proposed to the "rare male effect" in Drosophila is habituation to odorous cues (see Partridge & Hill 1984 for a discussion on mechanisms behind rare male effect), the mechanism proposed here follows by symmetry: in Drosophila contact pheromones are released by the males (Fletcher 1977).

The appearance of Lack's (1947) paper "On the significance of clutch size", initiated much research, thought and field work, on evolutionary aspects of reproduction. His theory focused on very simple and basic things, like food availability and the parents ability to nourish and protect their young. He hypothesized that birds should lay that number of eggs which on the average maximizes the production of young. In the mid-sixties enough data had been gathered showing that the corollary from Lack's hypothesis that the average clutch size in an area should coincide with the most productive, could be rejected. This led Williams (1966) to propose a refinement of Lack's hypothesis. Williams' idea was that there is a trade off between present reproduction and future survival; the reproductive effort model. This novel idea seemed to explain the observation that the most common clutch size usually is less than the most productive one (see Klomp 1970). The effect of Williams refinement was that Lack's hypothesis became a part of a much more general structure ideas, the theory of optimal life histories (see Stearns 1976, 1977 and Charlesworth 1980 for reviews).

Well aware of the fact that this is the place where it belongs, the incentive for my work has been a wish to build simple models, focusing on measurable things rather than environmental stochasticity and the like (cf. Stearns 1976). Thus I have chosen to investigate the impact of various types of mortality factors on optimal clutch size. The basic assumption is that what is maximized is the production of young each breeding occasion. This poses no problem, because the effect of a reduction in clutch size of the type outlined by Williams ought to be the same as an experimental reduction of the clutch size with one or a few eggs (see paper iv).

The two papers included in the thesis are building on the same ideas, but looking upon the problem from two different points of view. In paper iii I investigate the evolution of clutch size, whereas paper iv is devoted to the consequences of optimality.

Evolution of clutch size - Lack (1947) strongly emphasized the availability of food as an ultimate limiting factor in the determination of clutch size. He rejected both predation and egg infertility (Lack 1947a) as possible factors, and in these early works he never considered the possibili-

ty that mortality factors could act in concert and that in this "web of causation" some factors could be important, although they were not the limiting factor.

This problem is investigated in paper iii, in which I take Lack's hypothesis for granted in that I assume the existence of a most productive brood size, owing to food shortage, as a kind of background. On this I superimpose other factors, predation and egg infertility. The former is thought to act in a clutch size dependent fashion (its clutch size dependence is multiplicative in the terminology used in paper iv). Egg infertility is clutch size independent, but its action causes a variation in brood size and clutches may therefore often contain a less than optimal number of chicks. A review of data for four species shows that in no case the distribution of unhatched eggs differs significantly from the expected binomial.

This knowledge justifies the use of the binomial distribution for calculating the expected production of young from a single clutch size, assuming a linear function for describing the decline in survival with increasing clutch size. The derived function for the expected production, allows me to calculate the incidence of unhatched eggs at which it becomes advantageous to increase the clutch size with one or more eggs. This might be called compensatory egg laying. It is the very opposite to bet-hedging (Cohen 1966, Stearns 1976), in the sense that in the latter the environmental conditions varies, whereas the creature's phenotype is predictable. It may then adopt a pessimistic strategy and decrease its clutch size. In compensatory egg-laying, the environment is thought to be predictable, whereas there is some randomness in the determination of the creature's phenotype. This may lead to the adoption of an optimistic strategy.

Van Noordwijk & Scharloo (1981) have shown that inbreeding in great tit leads to an increase in the incidence of unhatched eggs. It is hard to evaluate whether or not compensatory egg-laying occur among inbred pairs. Presumably it does not, since clutch size does not correlate with the pairs coefficient of consanguinity. However, one would expect that the occurrence of unhatched eggs would have the same effect as an experimental reduction of clutch size, i.e., an increase in survival and a decrease in production in comparison with clutches of the same original size (this can be seen by analysing the data of e.g., Högstedt 1980). The inbred clutches in Van Noordwijk's & Scharloo's study have a higher production than clutches of comparable size with no inbreeding.

The effect of predation is to decrease the optimum, and the most note-

worthy conclusion is that much less predation is needed to push the optimum from the most productive brood size, than to make this factor the limiting one in itself. Finally I show that the effects of egg infertility and predation may balance each other, and greater forces may thus be needed to push the optimum from the most productive brood size.

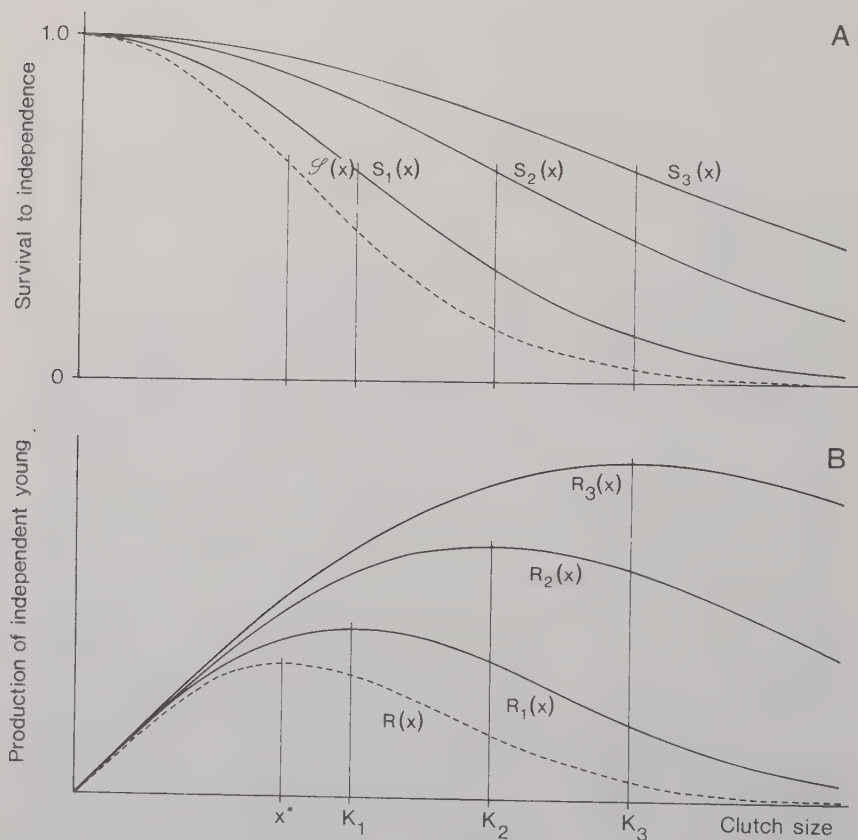


Figure 4. (A) Curves showing the clutch size dependence of three mortality factors (solid graphs) and how they combine to the overall survival (dashed curve). If each of these factors could be isolated, the optimal clutches would be (respectively) K_1 , K_2 and K_3 , corresponding to the peaks of the three production curves in (B). The optimum clutch size when the three factors act in concert rather than one at a time [x^* , given by the peak of the dashed production graph in (B)] is always less than the lowest K -value. The reproductive success for clutches of the optimum size is given by the weighted geometric mean of the values $S_1(K_1)$, $S_2(K_2)$ and $S_3(K_3)$.

Evolutionary regulation of reproductive success. - In paper iv I investigate the joint evolutionary regulation of clutch size and reproductive success (reproductive success is defined as the ratio between number of independent young produced by a pair and their clutch size). I consider two types of models. The first (model 1) takes into account an arbitrary number of mortality factors, all of which are assumed to act in a clutch size dependent fashion. In the second model (model 2) I discuss the consequences of a division of all deaths into two categories, with respect to their level of action. That is, I assume that there is a set of mortality factors causing total failures, and another set that causes partial losses, of the clutch. In both types of models I concentrate on clutch size dependent factors.

Model 1 is used for deriving a number of general theorems. I introduce two abstract quantities characterizing each mortality factor. First, the most productive clutch sizes that should evolve in response to each factor acting one at a time. I denote this K_i for factor i . Secondly, I use the survival rates of the young in these hypothetical states. I denote the survival rate $S_i(x)$ of young in clutches of the size x in the hypothetical state that should arise if factor i acts alone (the notation in paper iv is not exactly the same). By using these, a bit abstract tools, I am able to show that the clutch size that evolves when all factors act in concert is always less than the least of these K_i values, that is, this factor is the limiting (Fig. 4). I also show that this factor not only limits the actual clutch size, but also determines its range of variation. Finally, it turns out that reproductive success at optimum clutch size is the weighted geometric mean of the survival rates that should have evolved if each factor acted in isolation [$S_i(K_i)$].

The theorems derived by using model 1, are then used in model 2. In this I apply an extension of a probability model called the pure death process in the mathematical statistics literature, for analyzing the variation in production of young from a single clutch size.

This analysis is then used for making a number of qualitative predictions on the variation of reproductive success under various conditions, including the outcomes of experimental manipulations of brood size.

Nilsson (1858) and Palmén (1874) were the first (known to me) to point out that bird species often might be divided into populations with separate breeding and overwintering sites. Nilsson proposed that the wintering quarters of a species are situated in the same latitudinal sequence as the breeding grounds, whereas Palmén argued that the opposite pattern (i.e., wintering grounds in the reverse sequence as the breeding grounds), could be observed in many species. Salomonsen (1955) concluded in his review that, while leap frog tendencies are relatively common, chain migration "is not so commonly established as should be expected".

Salomonson (1955) as well as more recent authors (e.g., Alerstam & Högstedt 1980, 1985, Pienkowski et al. 1985) stressed the importance of intraspecific competition as an ultimate selection pressure causing geographical segregation between populations adopting different migration routes. Alerstam & Högstedt (1980) focused on competition on the breeding grounds, whereas Pienkowski et al. (1985) argued that it is well established fact that among shorebirds there is an asymmetric intra-specific competition on the wintering sites. According to them this factor presumably is more important than competition on the breeding sites.

In paper v, two models are proposed for the population dynamics of migratory bird species in seasonal environments. The first is used for investigating the problem of latitudinal and the second the problem of longitudinal geographical population segregation.

The former model builds upon the following assumptions: 1. Asymmetric competition is assumed, such that individuals travelling a shorter distance and arriving earlier to the destination have a competitive edge in interactions with individuals travelling longer and arriving later. The degree of advantage (or disadvantage) is correlated to the difference in distance travelled, of the interacting individuals. 2. Migration costs are included by means of a distance dependent survival rate. It is assumed that the costs are equal during spring and autumn. 3. There are latitudinal gradients in breeding and wintering suitability. These gradients have thresholds, such that the breeding suitability is zero south of a certain latitude and the wintering suitability is similarly zero north of a certain latitude. For simplicity we use a model with five discrete equidistant sites. The thresholds are chosen in a way allowing a resident population in the central point. 4. During breeding and overwintering there are density dependent declines in breeding and wintering suitabilities. The

mathematical formulation of this is similar to the conventional Volterra-Lotka competition equations.

The model was investigated numerically and all possible combinations of absence and presence of gradients in breeding and wintering suitability and absence and presence of asymmetry in the competitive interactions occurring during breeding and wintering. We started the simulations with all migration routes occupied (with five sites and the constraint that birds do not move further north during autumn and further south during spring, this leads to a system of 15 non-linear difference equations) and iterated the system for 150-300 generations. After this length of time the system was generally stable, and it had then reached a state with at least some degree of geographical segregation. More complicated behaviours were observed when a gradient was assumed during one season, and asymmetric competition during the other. This situation was characterized by oscillations, both in space and time.

Leap-frog patterns arose when there was asymmetry during both breeding and overwintering, and gradients under no more than one of these seasons. In the remaining cases chain migration was the dominating pattern. Inclusion of migration costs in absence of asymmetry in the competitive interactions leads to chain migration, but when superimposed on a system with asymmetry it was not powerful enough to change the pattern. The effect of a very high migration cost on a leap-frog pattern, was to change the geographical distribution of the species.

A related problem is: What are the conditions for a stable longitudinal segregation, that is, what makes a migratory divide stable. We used a model with 32 sites situated with equal distances on a single latitude. There were two large overwintering areas, thus we had 64 different migration routes (and as many non-linear difference equations). Inclusion of a migration cost was sufficient to cause a geographic segregation, and so was the inclusion of asymmetric competition (the latter occurred only if the difference in carrying capacity between the wintering sites was not too large).

To sum up: Asymmetric competition seems to be a crucial factor both for the origin and the stability of bird migration patterns. This is particularly true for leap-frog migration, whereas chain-migration can arise merely as a consequence of migration costs. Longitudinal segregation can arise in several ways and is much easier to grasp, as it is either a kind of optimization problem (it does not pay to travel longer than to a certain point) or a question of competitive exclusion.

Acknowledgement. I thank Björn von Rosen for letting me reproduce his drawing "The solitaire" on the cover. Just en passant, a translation of his poem accompanying it.

THE SOLITAIRE

No contemporary beings bear
a resemblance to the Solitaire.

Over cliff and bog on R union.
once it waddled, heavy. Now it's gone.

Never more it straddles cliffs and bogs.
Ships arrived. And sailors came - with dogs.

Crows abound in verey hemisphere.
Sparrows swarm. But not a Solitaire!

The Ecology Building is one of the few places these days where a solitaire can live safe among conspecifics.

I thank all my colleagues and the technical staff for help and support. I thank S. Douwes, G. Lindquist and Y. Zachrisson for the technical production of the booklet. Special thanks are due to my supervisors P. Brinck and N.C. Stenseth. T. Alerstam, C. L fstedt and N.C. Stenseth, are thanked for stimulating collaboration. Finally, T. Alerstam, O. Anderbrant, B.O. Bengtsson, B. Ebenman, G. H gstedt, J. Loman, J.- . Nilsson, M. Sandell, F. Schlyter, H. Smith, and N.C. Stenseth, have all read and made comments on parts of the thesis.

Gertrud Berger did not do any typing, but I thank her and my parents anyway.

REFERENCES

- Alerstam, T. & Högstedt, G. 1980. Spring predictability and leap-frog migration. - *Ornis Scand.* 11: 196-200.
- Alerstam, T. & Högstedt, G. 1985. Leap-frog arguments: reply to Pienkowski, Evans and Townshend. - *Ornis Scand.* 16: 71-74.
- Bjostad, L.B., Linn, C.E., Du, J.-W. & Roelofs, W.L. 1984. Identification of new sex pheromone component in *Trichoplusia ni*, predicted from biosynthetic precursors. - *J. Chem. Ecol.* 10: 1309-1323.
- Charlesworth, B. 1980. Evolution in age-structured populations. - Cambridge University Press, Cambridge.
- Cohen, D. 1966. Optimizing reproduction in a randomly varying environment. *J. Theoret. Biol.* 12: 119-129.
- Fletcher, B.S. 1977. Behavioral responses of diptera. In: Shorey, H.H. & McKelvey, Jr, J.J. eds, Chemical control of insect behavior. - John Wiley & Sons, New York.
- Haynes, K.F., Gaston, L.K., Mistrof Pope, M. & T.C. Baker. 1984. - Potential for evolution of resistance to pheromones: Interindividual and interpopulational variation in chemical communication of pink bollworm moth. - *J. Chem. Ecol.* 10: 1551-1565.
- Högstedt, G. 1980. Evolution of clutch size in birds: Adaptive variation in relation to territory quality. - *Science* 210: 1148-1150.
- Kennedy, J.S. & Marsh, D. 1974. Pheromone-regulated anemotaxis in flying moths. - *Science* 184: 999-1001.
- Klomp, H. 1970. The determination of clutch-size in birds, a review. - *Ardea* 58: 1-120.
- Lack, D. 1947. The significance of clutch-size, Part I. - *Ibis* 89: 302-352.
- Lack, D. 1947a. The significance of clutch-size in the partridge (*Perdix perdix*). - *J. Anim. Ecol.* 16: 19-25.
- Lawlor, L. & Maynard Smith, J. 1976. The coevolution and stability of competing species. - *Am. Nat.* 110: 79-99.
- Levins, R. 1968. Evolution in changing environments. - Princeton University Press, Princeton.
- Linn, C.E., Bjostad, L.-B., Du, J.-W. & Roelofs, W.L. 1984. Redundancy in a chemical signal: Behavioral responses of male *Trichoplusia ni* to a 6-component sex pheromone. - *J. Chem. Ecol.* 10: 1635-1657.
- MacArthur, R. & Levins, R. 1964. Competition, habitat selection and character displacement. - *Proc. Natl. Acad. Sci.* 48: 1893-1897.
- Maynard Smith, J. 1982. Evolution and the theory of games. - Cambridge University Press, Cambridge.
- Nilsson, S. 1858. Skandinavisk fauna, fåglarne. Första bandet. - Gleerups, Lund.
- Palmén, J.A. 1874. Om foglarnes flyttningsvägar. - Frenckell. Helsinki.
- Partridge, L. & Hill, W.G. 1984. Mechanisms for frequency dependent mating success. - *Biol. J. Linn. Soc.* 23: 113-132.
- Pienkowski, M.W., Evans, P.R. & Townshend, D.J. 1985. Leap-frog and other migration patterns of waders: A critique of the Alerstam and Högstedt hypothesis, and some alternatives. *Ornis Scand.* 16: 61-70.
- Salomonsen, F. 1955. The evolutionary significance of bird-migration. - *Dan. Biol. Medd.* 22(6): 1-61.
- Shorey, H.H. 1977. Manipulation of insect pests of agricultural crops. In: Shorey, H.H. & McKelvey, Jr, J.J. Chemical control of insect behavior. - John Wiley & Sons, New York.
- Slatkin, M. 1980. Ecological character displacement. - *Ecology* 61: 163-177.

- Sower, L.L., Gaston, L.K. & Shorey, H.H. 1971. Sex pheromones of noctuid moths. XXVI. Femal release rate, male response threshold and communication distance for Trichoplusia ni. - Ann. Entomol. Soc. Amer. 64: 1448-1456.
- Stearns, S.C. 1976. Life history tactics: a review of the ideas. - Quart. Rev. Biol. 51: 3-47.
- Stearns, S.C. 1977. The evolution of life history traits: A critique of the theory and a review of the data. - Ann. Rev. Ecol. Syst. 8: 145-171.
- Van Noordwijk, A.J. & Scharloo, W. 1981. Inbreeding in an Island population of the great tit. - Evolution 35: 647-688.
- Wall, C. & Perry, J.N. 1978. Interactions between pheromone traps for the pea moth Cydia nigriana (F.). Ent. Exp. & Appl. 24: 155-162.
- Wall, C. & Perry, J.N. 1980. Effects of spacing and trap number on interactions between pea moths pheromone traps. - Ent. Exp. & Appl. 28: 313-321.
- West-Eberhard, M.J. 1984. Sexual selection, competitive communication and species specific signals in insects. In: T. Lewis ed.: Insect communication. - Academic Press, Orlando.
- Williams, G.C. 1966. Natural selection, the cost of reproduction and a refinement of Lack's principle. - Am. Nat. 100: 687-690.

Coevolution of Competing Species: Ecological Character Displacement

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Character displacement of competing species is studied. A model, originally developed by MacArthur and Levins (*Proc. Natl. Acad. Sci. USA* **51** (1964), 1207–1210) and further analyzed by Lawlor and Maynard Smith (*Amer. Nat.* **110** (1976), 70–99), has been reanalyzed. In the present paper, a more formally correct analysis of the MacArthur–Levins model is provided. A standard population genetics approach to sexually reproducing populations is adopted. The same conclusion as proposed by Lawlor and Maynard Smith emerges; competition can lead only to character divergence. In our analysis we either require that allopatrically evolved consumer populations must be able to coexist at an ecologically stable equilibrium (hence, we require mutual invasibility), or consider the feasibility of allopatric equilibria. © 1985 Academic Press, Inc.

INTRODUCTION

Observed character divergence is often reported to result from interspecific competition (e.g., Brown and Wilson, 1956; Hutchinson, 1959; Schoener, 1970; McNab, 1971; Pianka, 1973, 1974; Huey *et al.*, 1974; Cody, 1974; Grant, 1972, 1975; Fenchel, 1975a, 1975b; Fenchel and Kofoed, 1976). However, many of these studies, particularly the older ones, may be criticized (e.g., Grant, 1972): not all reported cases of character divergence need to be the result of competition.

The concept of character displacement has stimulated much theoretical work. Since the seminal paper by MacArthur and Levins (1964), many papers have been published; for review, see Slatkin and Maynard

Smith (1979) and Roughgarden (1979). The model formulated by MacArthur and Levins (1964; see also 1967) differs from most other evolutionary models of competing species (e.g., MacArthur and Wilson, 1967; Grant, 1972; Cody, 1973, 1974), as it explicitly describes the dynamics of the resources for which there is competition. As demonstrated by Lawlor and Maynard Smith (1976), this extension is not trivial; furthermore, it is not obvious whether conclusions regarding the outcome of coevolution are indifferent to this extension (Schoener, 1969; Slatkin, 1980).

An important reanalysis of the MacArthur-Levins model was published by Lawlor and Maynard Smith (1976). This reanalysis was necessary since the coevolved strategies (under competition) deduced by MacArthur and Levins (1964) were the same as those found in the absence of competition (see Lawlor and Maynard Smith, 1976). This strange result seems to rest on the fact that the two competing species are identical and that, accordingly, there is no difference between intra- and interspecific competition. The model reported by Schoener (1969)—producing the same result as found by MacArthur and Levins—seems to be bothered by the same difficulty.

By assuming that each species has its own fitness set (Levins, 1968), Lawlor and Maynard Smith (1976) arrived at a different conclusion: coevolution of competing species is only expected to lead to character divergence. This latter conclusion is consistent with several other theoretical investigations (e.g., Bulmer, 1974; Fenchel and Christiansen, 1977; Christiansen and Fenchel, 1977).

Unfortunately, the conclusion drawn by Lawlor and Maynard Smith (1976)—saying that character divergence is the only possible evolutionary outcome of competition—is based upon a rather informal and vague argument (see their Appendix B). The first objective of this paper is therefore to perform a thorough reanalysis of the MacArthur-Levins model by using the approach suggested by Lawlor and Maynard Smith (1976). In this reanalysis we also extend the original MacArthur-Levins model to be applicable to sexually reproducing species; that is, the phenotypic model analyzed by Lawlor and Maynard Smith (1976) is extended to a population genetic model for a pair of species without age structure. The second objective of this paper is to investigate how a coevolutionary competition theory based on renewable resources will differ from the traditional one which is based on Gaussian resource spectra.

THE MODEL

A one-locus, two allele, model is assumed for describing the consumer's efficiencies of capturing and consuming its resources. Consumers are assumed to be resource-limited whereas resources are assumed to be self-

regulated. Hence, the fitness of a given consumer genotype depends on its efficiencies in utilizing available resources, and the amount of resources available.

Fitness

We define the fitness of genotype (k, l) ($k = 1, 2$ and $l = 1, 2$) of the i th consumer species as

$$m_{kli} = a_{kli1} w_1 R_1 + a_{kli2} w_2 R_2 - T_i, \quad (1)$$

where R_1 and R_2 are the available amounts of resource 1 and 2, respectively; a_{klij} measures the efficiency by which the consumer kli utilizes resource j , and w_j is the "value" of resource j .

The first two terms in (1) may be interpreted as the birth rate of consumer kli , whereas the last term, T_i , represents the death rate of the i th species, regardless of its genotype (alternatively, T_i may be interpreted as a threshold food requirement).

Our definition of the Malthusian parameter m_{kli} , given by (1) is of the same form as the one used for density-independent selection (see, e.g., Crow and Kimura, 1970); certainly this is a reasonable feature since the consumer species are assumed to be limited only by their resources.

Mean fitness of the i th consumer species is given by

$$\bar{m}_i = p_i^2 m_{11i} + 2 p_i q_i m_{12i} + q_i^2 m_{22i}, \quad (2)$$

where p_i is the frequency of allele 1 in species i and $q_i = 1 - p_i$ is the corresponding frequency of allele 2. Substituting individual fitness functions (1) into (2) and collecting terms, we then obtain

$$\bar{m}_i = \bar{a}_{i1} w_1 R_1 + \bar{a}_{i2} w_2 R_2 - T_i, \quad (3)$$

where $\bar{a}_{ij}$ is the mean exploitation efficiency, which is given by

$$\bar{a}_{ij} = p_i^2 a_{11ij} + 2 p_i q_i a_{12ij} + q_i^2 a_{22ij}. \quad (4)$$

Following standard population genetics theory (e.g., Crow and Kimura, 1970), changes in the i th species population density x_i and its corresponding gene frequency p_i are given by

$$\begin{aligned} dx_i/dt &= x_i \bar{m}_i \\ dp_i/dt &= \frac{1}{2} p_i q_i [p_i(m_{11i} - m_{12i}) + q_i(m_{12i} - m_{22i})] \\ &= \frac{1}{2} p_i q_i (d\bar{m}_i/dp_i). \end{aligned} \quad (5)$$

Combining (5) with the dynamics of the resources, we obtain the following

system of six simultaneous differential equations describing changes in fitness of the interacting species:

$$\begin{aligned}
 (dx_1/dt)/x_1 &= \bar{a}_{11}w_1R_1 + \bar{a}_{12}w_2R_2 - T_1 \\
 (dx_2/dt)/x_2 &= \bar{a}_{21}w_1R_1 + \bar{a}_{22}w_2R_2 - T_2 \\
 (dR_1/dt)/R_1 &= \varphi_1(R_1) - \bar{a}_{11}x_1 - \bar{a}_{21}x_2 \\
 (dR_2/dt)/R_2 &= \varphi_2(R_2) - \bar{a}_{12}x_1 - \bar{a}_{22}x_2 \\
 dp_1/dt &= \frac{1}{2}p_1q_1[w_1R_1(d\bar{a}_{11}/dp_1) + w_2R_2(da_{12}/dp_1)] \\
 dp_2/dt &= \frac{1}{2}p_2q_2[w_1R_1(d\bar{a}_{21}/dp_2) + w_2R_2(d\bar{a}_{22}/dp_2)],
 \end{aligned} \tag{6}$$

where φ_j is the density-dependent specific renewal rate of resource j . We assume φ_j to be a monotonically decreasing function of R_j such that the renewal rate is positive when the resource density is less than the carrying capacity (K_j) of resource j and negative when the density is greater than K_j .

Let α_{kij} denote the additive effect of an allele k on the i th species' efficiency in utilizing resource j ; let further δ_{klj} denote the deviation due to dominance so that $a_{klj} = \alpha_{kij} + \alpha_{lij} + \delta_{klj}$ (we ignore all environmental effects). Utilizing least square estimates (see Roughgarden, 1979), we obtain

$$\begin{aligned}
 \alpha_{1ij} &= p_i a_{11ij} + q_i a_{12ij} - \bar{a}_{ij}/2 \\
 \alpha_{2ij} &= p_i a_{12ij} + q_i a_{22ij} - \bar{a}_{ij}/2.
 \end{aligned} \tag{7}$$

An Ecological Analogue to Fisher's Fundamental Theorem of Natural Selection

We can now formulate an ecological analogue to Fisher's (1930) fundamental theorem of natural selection. In order to do so, we must introduce the additive effect on fitness of the k th allele of species i , μ_{ki} , defined by the relation

$$\mu_{ki} = \alpha_{kij}w_1R_1 + \alpha_{ki2}w_2R_2 - T_i/2. \tag{8}$$

By taking the time derivative of the mean fitness function (3) and observing that the change in gene frequency can be expressed by (6), we obtain

$$\begin{aligned}
 d\bar{m}_i/dt &= \frac{1}{2}p_iq_i[w_1R_1(d\bar{a}_{i1}/dp_i) + w_2R_2(d\bar{a}_{i2}/dp_i)]^2 \\
 &\quad + \bar{a}_{i1}w_1(dR_1/dt) + \bar{a}_{i2}w_2(dR_2/dt).
 \end{aligned} \tag{9}$$

In Appendix A we demonstrate that the first term of the right-hand side of (9) is identical to the additive variance in fitness which is given by

$$\begin{aligned}
 V_{Am_i} &= w_1^2R_1^2V_{Aa_{i1}} + 2w_1w_2R_1R_2\text{cov}_{Aa_1a_2} \\
 &\quad + w_2^2R_2^2V_{Aa_{i2}},
 \end{aligned} \tag{10}$$

where V_A and cov_A denote the additive variance and the additive covariance of the trait referred to by the subscript. The additive covariance, cov_A , is defined as the covariance between the additive effects of the traits. Our concept of additive covariance differs from a similar one discussed by Crow and Nagylaki (1976) who were concerned with the rate of change of a trait correlated with fitness: their "genetic covariance" is the covariance between the average excess in fitness and the additive effect of the trait.

Combining (9) and (10) the ecological analogue to Fisher's fundamental theorem emerges.

The Mean Strategy Curve

We have assumed that the consumer's efficiencies of capturing and consuming their prey is genetically determined by pleiotropic alleles at a single locus. The mean efficiencies $(\bar{a}_{i1}, \bar{a}_{i2})$ can be regarded as a vector-valued function of the gene frequency p_i , which can be drawn as a curve in the $(\bar{a}_{i1}, \bar{a}_{i2})$ -plane. This is called the *mean strategy curve* in the following, and is mathematically equivalent to the fitness set function (see Stenseth, 1984). Levins' (1968) concept of fitness set introduced when discussing genetic constraints is similar to our concept of mean strategy curve.

THE EQUILIBRIUM PROPERTIES OF THE MODEL

The model has several equilibria; however, we are primarily concerned with only two: first, we have the interior equilibrium, corresponding to the case where the consumer species occur sympatrically; this we denote by $(x_1^{**}, x_2^{**}, R_1^{**}, R_2^{**}, p_1^{**}, p_2^{**})$. Second, there is a boundary equilibrium, in which each consumer occurs allopatrically; this we denote by $(x_i^*, R_i^*, R_j^*, p_i^*)$ for the i th consumer species.

In the following we give the results of the analysis of the model for the allopatric situation: they are, however, also valid for the sympatric case unless the contrary is stated.

A Genetic Analogue of the "Principle of Allocation"

If the evolutionary equilibrium is nontrivial (i.e., $p_i^* \neq 0$ and 1), the tangent to the population mean strategy curve must have a negative slope. This is so because from (6) we have that

$$w_1 R_1^* (d\bar{a}_{i1}/dp_i)_{p_i^*} = -w_2 R_2^* (d\bar{a}_{i2}/dp_i)_{p_i^*}, \quad (11)$$

where the derivatives are evaluated at the equilibrium gene frequency p_i^* . This gives a condition for the occurrence of an evolutionary equilibrium which is mathematically equivalent to the one derived by Lawlor and

Maynard Smith (1976): they found $d\bar{a}_{i2}/d\bar{a}_{i1} = -w_1 R_1^*/(w_2 R_2^*)$ (i.e., the mean strategy curve has a negative slope at equilibrium). Further, if the variance in the traits is largely additive, then the regression of the utilization efficiencies of one of the resources on those of the other will always be negative. This is so because a regression between their additive estimates has the following slope

$$\begin{aligned} \text{Cov}_{Aa_{i1}a_{i2}}/V_{Aa_{i2}} &\equiv (d\bar{a}_{i2}/dp_i)/(d\bar{a}_{i1}/dp_i) \\ &\equiv d\bar{a}_{i2}/d\bar{a}_{i1} = -[w_1 R_1^*/(w_2 R_2^*)] \end{aligned} \quad (12)$$

(see Appendix A for derivation), where the latter identity is only valid when $\bar{a}_{i1}$ is a strictly monotonic function.

Essentially, this is a reformulation of the "principle of allocation" (Cody, 1966) in terms of additive genetic variation.

Characteristics of the Equilibria

Mean fitness always increases in the neighborhood of an asymptotically stable equilibrium. This is so because from (9) and (10) we obtain our analogue to Fisher's fundamental theorem

$$d\bar{m}_i/dt = V_{Am_i} + \bar{a}_{i1}w_1(dR_1/dt) + \bar{a}_{i2}w_2(dR_2/dt), \quad (13)$$

where $dR_1/dt \approx 0$ and $dR_2/dt \approx 0$ close to equilibrium and where the additive variance in fitness V_{Am_i} is non-negative.

Natural selection will therefore maximize $\bar{m}_i$ as given by (3) constrained by the genetic system and the available genetically determined phenotypic variation. Therefore, in order to predict the equilibrium values of our evolutionary variables ($\bar{a}_{i1}$, $\bar{a}_{i2}$), we can employ the following optimization criterion.

By rearranging (3) and substituting R_1^* and R_2^* , we obtain the following adaptive function (compare Levins, 1968):

$$\bar{a}_{i2} = [(\bar{m}_i + T_i)/(w_2 R_2^*)] - [(w_1 R_1^*)/(w_2 R_2^*)] \bar{a}_{i1}. \quad (14)$$

From this we see that the evolutionary equilibrium ($\bar{a}_{i1}^*$, $\bar{a}_{i2}^*$) is characterized by a combination of efficiencies on the population mean strategy curve that is touched by the line defined by (14) and being as far away from the origin as possible (see Fig. 1a, b). Note that this procedure is independent of whether it is a boundary or an interior equilibrium which is under consideration. This implies that, in sympatry, the slopes of the two consumer species' adaptive functions must equal each other. It follows that polymorphism is possible under sympatry as well as allopatry only when

$$(d^2\bar{a}_{i2}/d\bar{a}_{i1}^2)_{p_i^*} < 0, \quad (15)$$

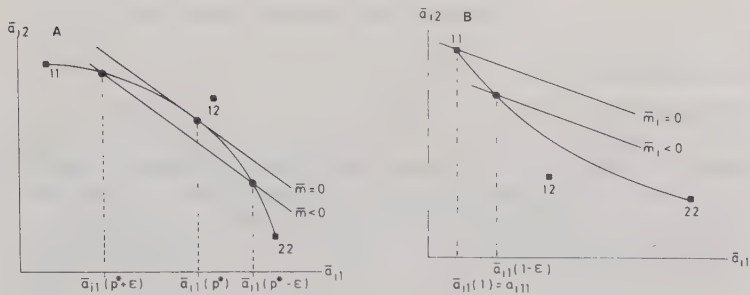


FIG. 1. Fitness sets and mean strategy curves. In (a) the mean strategy curve is convex and in (b) concave, so that in the former case a stable polymorphism is possible and in the latter one allele will go to fixation. ■'s represent the phenotypes corresponding to the genotypes 11, 12, and 22.

that is, (nontrivial) genetic equilibria ($p^* \neq 0$ and 1) exists only when the populations' mean strategy curves are convex (Fig. 1a). A sufficient condition for this to occur, is that the heterozygote's location in the phenotype set (see Maynard Smith, 1978) lies above and to the right of the line connecting the homozygotes' location in the phenotype set. This is likely to occur when the resources are similar in size and shape so that their utilization does not require two highly different sets of adaptations (compare MacArthur, 1972; Stenseth, 1984). This then, is a specification of an earlier phenotypic interpretation presented by MacArthur and Levins (1967) and MacArthur (1972).

The allopatric equilibrium is further characterized by the relation

$$\bar{a}_{11}^*/\bar{a}_{12}^* = \varphi_1(R_1^*)/\varphi_2(R_2^*). \quad (16)$$

This corresponds directly to an equivalent condition given by Lawlor and Maynard Smith (1976).

Uniqueness of Equilibria

From (14) it follows that the adaptive functions of the two consumer species are the same when their threshold food requirements are equal. Then, since the two mean strategy curves can have one and only one tangent in common, the mean strategies of the populations that coevolve under sympatry are unique. However, this property is a consequence of the genetic system assumed; multiple equilibria might well arise if the genetic system is assumed to be more complicated.

It seems plausible that the uniqueness of the sympatric equilibria may be retained when the thresholds of the consumers are different; however, this remains to be shown.

POSSIBLE AND IMPOSSIBLE PATTERNS OF COEVOLUTION

Mutual Invasibility

A reasonable criterion for judging whether or not the configurations in Fig. 2 are plausible is that the allopatrically evolved strategies must be mutually invadable; if not, subsequent coevolution is impossible. If one of the species (the i th, say) lives alone (e.g., on an island), we may assume that it will be at its ecological and evolutionary equilibrium (x_i^* , R_i^* , R_j^* , p_i^*).

Consider an island where species 1 lives alone at its equilibrium. Its dynamics are then described by

$$(dx_1/dt)/x_1 = \bar{a}_{11}^* w_1 R_1^* + \bar{a}_{12}^* w_2 R_2^* - T_1 = 0. \quad (17)$$

Consumer species 2 can invade this island if

$$(dx_2/dt)/x_1 = \bar{a}_{21}^* w_1 R_1^* + \bar{a}_{22}^* w_2 R_2^* - T_2 > 0. \quad (18)$$

By subtracting (17) from (18) we obtain

$$(\bar{a}_{21}^* - \bar{a}_{11}^*)[(w_1 R_1^*)/(w_2 R_2^*)]_{p_1^*} + (\bar{a}_{22}^* - \bar{a}_{12}^*) > (T_1 - T_2)/(w_2 R_2^*)_{p_1^*}. \quad (19)$$

An equivalent condition exists for the opposite case when species 1 attempts to invade an island inhabited exclusively by species 2. By combining these conditions and assuming that $T_1 = T_2$ (which means that both consumer species have approximately the same maintenance requirements), we obtain two conditions for mutual invasibility:

$$-[w_1 R_1^*/(w_2 R_2^*)]_{p_1^*} < (\bar{a}_{22}^* - \bar{a}_{12}^*)/(\bar{a}_{21}^* - \bar{a}_{11}^*) < -[w_1 R_1^*/w_2 R_2^*]_{p_2^*} \quad (20)$$

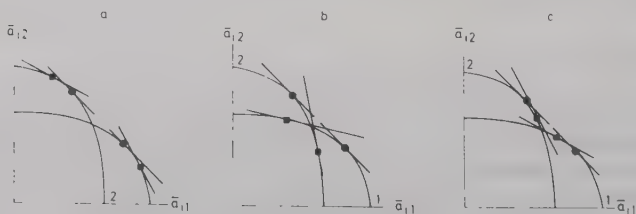


FIG. 2. Possible and impossible patterns of coevolution. Homozygotes are assumed to be specialists on either resource. ■'s represent the allopatrically evolved strategies and the ●'s the coevolved mean strategies: (a) depicts the convergent, (b) the crossover, and (c) the divergent case. Only the last configurations are plausible because they do not, as the other, violate the condition of mutual invasibility.

for $\bar{a}_{21}^* - \bar{a}_{11}^* > 0$ (see Fig. 2b), and

$$-|w_1 R_1^*/(w_2 R_2^*)|_{p_1} > (\bar{a}_{22}^* - \bar{a}_{12}^*)/(\bar{a}_{21}^* - \bar{a}_{11}^*) > |w_1 R_1^*/(w_2 R_2^*)|_{p_1}, \quad (21)$$

for $\bar{a}_{21}^* - \bar{a}_{11}^* < 0$ (see Figs. 2a, c).

These conditions are similar to the one given by Lawlor and Maynard Smith (1976, pp. 91–92; note the misprint in their equation (18)—a minus sign is lacking just after the first parenthesis in their equation). The geometric interpretation of (20) and (21) is clear from Fig. 3: these relations impose constraints on the magnitudes of the slopes of the consumers' adaptive functions in allopatry and the line that connects the two allopatrically evolved mean strategies.

That divergence is the only biologically plausible pattern of coevolution can now be seen by comparing the conditions for mutual invasibility with the relations given in Table 1. These are derived from Fig. 2 and are of two kinds. First, we have restrictions on the mean strategies derived by comparing the slopes of the lines from the origin to the equilibrium points $(\bar{a}_{11}^*, \bar{a}_{12}^*)$ and $(\bar{a}_{21}^*, \bar{a}_{22}^*)$; second, we have restrictions on the resource densities obtained by comparing the slopes of the adaptive functions of the two species. We see that the convergence and crossover cases are incompatible with our conditions given by (20) and (21).

As an example we discuss the crossover case: since $\bar{a}_{11}^* - \bar{a}_{21}^* < 0$, we have from (20) that

$$-|w_1 R_1^*/(w_2 R_2^*)|_{p_1} < -|w_1 R_1^*/(w_2 R_2^*)|_{p_2}. \quad (22)$$

The corresponding inequality in Table 1, derived from Fig. 2, is in the opposite direction; that is, a contradiction.

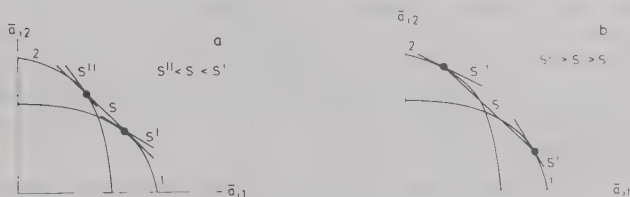


FIG. 3. Graphical interpretation of the conditions for mutual invasibility (Eqs. (20) and (21)). The ●'s represent the allopatric equilibrium mean strategies on curve 1 ($\bar{a}_{11}^*, \bar{a}_{12}^*$) and on curve 2 ($\bar{a}_{21}^*, \bar{a}_{22}^*$). It is assumed that the homozygotes adopt specialist's strategies. s' is the slope of the adaptive function of consumer 1, s'' the corresponding slope for consumer 2, and s is the slope of the line connecting the mean strategies. It follows that the configuration in (a) leads to stable coexistence.

TABLE 1
Analytical Description of the Patterns in Fig. 2

Type of evolution	Restrictions on the ESS-solution	Restrictions on the resource densities
Convergent	$(\bar{a}_{11}^*/\bar{a}_{12}^*)_{p_1} > (\bar{a}_{21}^*/\bar{a}_{22}^*)_{p_2}$	$- w_1 R_1^*/(w_2 R_2^*) _{p_1} < - w_1 R_1^*/(w_2 R_2^*) _{p_2}$
Crossover	$(\bar{a}_{11}^*/\bar{a}_{12}^*)_{p_1} < (\bar{a}_{21}^*/\bar{a}_{22}^*)_{p_2}$	$- w_1 R_1^*/(w_2 R_2^*) _{p_1} > - w_1 R_1^*/(w_2 R_2^*) _{p_2}$
Divergent	$(\bar{a}_{11}^*/\bar{a}_{12}^*)_{p_1} > (\bar{a}_{21}^*/\bar{a}_{22}^*)_{p_2}$	$- w_1 R_1^*/(w_2 R_2^*) _{p_1} > - w_1 R_1^*/(w_2 R_2^*) _{p_2}$

Lawlor and Maynard Smith Revisited

Lawlor and Maynard Smith (1976) suggested, without giving a convincing argument, the same contradiction as derived above. They did not state that the crossover and convergent cases contradicted the condition for mutual invasibility (which they had, in fact, derived). Lawlor and Maynard Smith (1976) conjectured that those configurations of allopatrically evolved populations being evolutionarily stable strategies (or ESS; see Maynard Smith, 1982) which would lead to character convergence or crossover due to competition in sympatry (Fig. 2b, c) could not arise. Lawlor and Maynard Smith (1976) suggested this to be impossible for "reasonable renewal dynamics for the resources." Unfortunately, they did neither specify nor justify this statement.

In order to better understand the meaning of this statement by Lawlor and Maynard Smith, we shall also consider the convergent case: Assume that consumer species 2 is living alone and that it is more specialized on resource 2 than it would be at a sympatric equilibrium. Hence, $\bar{a}_{21}^*/\bar{a}_{22}^* < 1$. If w_1 and w_2 are roughly equal, we have from Table 1 that $R_1^*/R_2^* < 1$. This means that, although the consumer feeds more on resource 2 than 1, the former resource has a higher density than the latter. Lawlor and Maynard Smith *felt* that the opposite would be true if reasonable resource dynamics were assumed. Using (16), we have that $\phi_1(R_1^*)/\phi_2(R_2^*) < 1$. If the shape of the ϕ functions (i.e., the resource dynamics) is fairly similar, the opposite should be true for the reasons given by Lawlor and Maynard Smith, unless the values of both functions are less than zero. If so, $\phi_1(R_1^*) > \phi_2(R_2^*)$ under the assumption that $R_1^* > R_2^*$.

A similar proof can be given for the crossover case.

DISCUSSION AND CONCLUSIONS

We have formulated a population genetics model analogous to the ESS model presented by Lawlor and Maynard Smith (1976). When comparing the two models, we see that the ecological predictions are the same. It also

turns out that some assumptions made by Lawlor and Maynard Smith may be identified as results emerging from our analysis. The obvious reason for this is that their model assumes implicitly a certain genetic system in order for it to work for a sexually reproducing species, whereas we have made such genetic assumptions explicit.

Levin and Udovic (1977) criticized the ecological optimization procedure employed by Lawlor and Maynard Smith for being valid only in the special case of a genetic equilibrium being proof against invasion by any mutant allele. Our analysis suggests that this criticism is not as generally valid as implied by Levin and Udovic. The only case in which our model has an equilibrium that is stable in the sense of Lawlor and Maynard Smith occurs when the mean strategy curve is concave (Fig. 1b); this is indeed an unfavourable case for invasion of mutants.

The reason why the criticism of Levin and Udovic (1977) is invalid in our case, is that the present model retains—in a mathematical sense—the simple properties of density-dependent selection in spite of the fact that the different phenotypes do not compete on an equal basis. Ecologically our model corresponds to a situation with both within and between species frequency dependences (see Slatkin and Maynard Smith, 1979): the more similar phenotypes compete more intensively with each other than do more dissimilar ones; this is true for competition between as well as within species, and not only between species as in the model proposed by Roughgarden (1976). It is this absence of intraspecific frequency dependence—again in a mathematical sense—that makes it possible to derive an ecological analogue to Fisher's (1930) fundamental theorem of natural selection; an "*F*-theorem" has previously also been derived by León and Charlesworth (1978) for coevolutionary models involving density-dependent selection only. This makes it possible to show that fitness always increases in the neighborhood of equilibrium, given that there is no deterioration of the environment (leading, e.g., to reduced densities of the resources).

Although we arrive at the same ecological predictions as Lawlor and Maynard Smith (1976), our arguments are different: their conclusion saying that divergent character displacement is the only possible outcome of coevolution was not based on a formal proof but on a heuristic argument. However, we have been able to show that

- (i) no feasible allopatric evolutionarily and ecologically stable equilibrium exists for a consumer which is more specialized on a certain resource than is a consumer living together with a competitor; and
- (ii) two allopatrically evolved consumer species of this kind referred to under (i) above, can neither coexist nor coevolve.

One of these points might seem sufficient for excluding the possibility of character convergence. Unfortunately, we have not been able to make a

general analysis. However, by making different simplifications in the two cases we gain in generality.

Recent theoretical studies of competing species suggest that convergence in fact may be a possible outcome of coevolution (Slatkin, 1980). One of the main themes in Slatkin's paper is that the actual outcome is determined by the balance between two selective pressures; first, the convergent pressure imposed by the bell-shaped resource spectrum, and, second, a divergent pressure caused by other selective pressures due to competition. The latter is required by Grant (1972) as a criterion for accepting a shift in character state of a species as character displacement. But, nevertheless, the endpoint of the process described by Slatkin is determined by coevolution: whether or not this shall be labelled character convergence is a matter of taste.

Our results suggest that the *sympatrically* evolved strategies constitute the utmost degree of specialization that a species can achieve and still exist at an ecological *allopatric* equilibrium. Beyond that limit there is no feasible equilibrium. What features of our model give rise to this limit? The answer seems to be the assumption of "reasonable renewal dynamics for the resources" (see Lawlor and Maynard Smith, 1976). Although our two resources, admittedly, make a poor resource spectrum, this assumption is a step towards realism when compared with the conventional bell jar in which theoreticians usually keep their competing species. It may be that convergence as an outcome of coevolution is a product of the assumption of an *inanimate* resource spectrum.

APPENDIX A:

THE COMPONENTS OF THE VARIANCE OF FITNESS

Let p_{kli} be the frequency of genotype (k, l) in the i th species. Then, by definition (Roughgarden, 1979), the additive variance is given as

$$V_{Am_i} = \sum_{kl} p_{kli} (\mu_{ki} + \mu_{li} - \bar{m}_i)^2. \quad (A1)$$

By substituting (8) and (9) and collecting terms we see that

$$\begin{aligned} V_{Am_i} = & w_1^2 R_1^2 \sum_{kl} p_{kli} (\alpha_{ki1} + \alpha_{li1} - \bar{a}_{i1})^2 \\ & + 2w_1 w_2 R_1 R_2 \sum_{kl} p_{kli} (\alpha_{ki1} + \alpha_{li1} - \bar{a}_{i1}) \\ & \cdot (\alpha_{ki2} - \alpha_{li2} - \bar{a}_{i2}) \\ & + w_2^2 R_2^2 \sum_{kl} p_{kli} (\alpha_{ki2} + \alpha_{li2} + \bar{a}_{i2})^2. \end{aligned} \quad (A2)$$

Hence, by the definitions of variance and covariance, we have

$$V_{Am_i} = (w_1 R_1)^2 V_{Aa_{i1}} + 2w_1 w_2 R_1 R_2 \text{Cov}_{Aa_{i1}a_{i2}} + (w_2 R_2)^2 V_{Aa_{i2}}. \quad (\text{A3})$$

We now list some useful formulas for the additive variance and covariances and also the derivative of $\bar{a}_{ij}$ with respect to p_i . These formulas we derive from (A1), (A2), and (8). The additive variance of resource j by the i th consumer on the efficiency of utilization is given by

$$V_{Aa_{ij}} \equiv 2p_i q_i (\alpha_{1ij} - \alpha_{2ij})^2. \quad (\text{A4})$$

The additive covariance is given by

$$\text{Cov}_{Aa_{ij}} \equiv 2p_i q_i (\alpha_{1i1} - \alpha_{2i1})(\alpha_{1i2} - \alpha_{2i2}). \quad (\text{A5})$$

Finally, the derivative of $\bar{a}_{ij}$ with respect to p_i is given by

$$\begin{aligned} d\bar{a}_{ij}/dp_i &\equiv 2[p_i(a_{1ij} - a_{12i}) + q_i(a_{12i} - a_{22i})] \\ &= 2(\alpha_{1ij} - \alpha_{2ij}). \end{aligned} \quad (\text{A6})$$

By combining the formulas listed above we obtain

$$V_{A\bar{a}_{ij}} = \frac{1}{2} p_i q_i (d\bar{a}_{ij}/dp_i)^2. \quad (\text{A7})$$

$$\text{Cov}_{Aa_{i1}a_{i2}} \equiv \frac{1}{2} p_i q_i [(d\bar{a}_{i1}/dp_i)(d\bar{a}_{i2}/dp_i)]. \quad (\text{A8})$$

Hence,

$$\text{Cov}_{Aa_{i1}a_{i2}}/V_{Aa_{i1}} \equiv (d\bar{a}_{i2}/dp_i)/(d\bar{a}_{i1}/dp_i). \quad (\text{A9})$$

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REFERENCES

- BROWN, J., AND WILSON, E. O. 1956. Character displacement, *Syst. Zool.* 5, 49-64.
 BULMER, M. G. 1974. Density-dependent selection and character displacement. *Amer. Nat.* 108, 45-58.
 CODY, M. L. 1966. A general theory of clutch size. *Evolution* 20, 174-184.

- CODY, M. L. 1973. Character convergence, *Ann. Rev. Ecol. Syst.* **4**, 189–211.
- CODY, M. L. 1974. "Competition and the Structure of Birds Communities," Princeton Univ. Press, Princeton, N. J.
- CHRISTIANSEN, F. G., AND FENCHEL, T. M. 1977. "Theories of Populations in Biological Communities." Springer-Verlag, Heidelberg.
- CROW, J. F., AND KIMURA, M. 1970. "An Introduction to Population Genetics Theory," Harper & Row, New York.
- CROW, J. F., AND NAGYLAKI, T. 1976. The rate of change of a character correlated with fitness, *Amer. Nat.* **110**, 207–213.
- FENCHEL, T. M. 1975a. Factors determining the distribution patterns of mud snails (Hydrobiidae). *Oecologia (Berlin)* **20** 1–17.
- FENCHEL, T. M. 1975b. Character displacement and coexistence in mud snails (Hydrobiidae), *Oecologia (Berlin)* **20**, 19–32.
- FENCHEL, T. M., AND CHRISTIANSEN, F. G. 1977. Selection and interspecific competition, *Biometrics* **19**, 477–498.
- FENCHEL, T. M., AND KOFOED, L. H. 1976. Evidence for exploitative interspecific competition in mud snails (Hydrobiidae). *Oikos* **27**, 367–376.
- FISHER, R. A. 1930. "The Genetical Theory of Natural Selection," Oxford Univ. Press (Clarendon), Oxford.
- GRANT, P. R. 1972. Convergent and divergent character displacement, *Biol. J. Linn. Soc.* **4**, 39–68.
- GRANT, P. R. 1975. The classical of character displacement, in "Evolutionary Biology" (T. Dobzhansky, M. K. Hecht, and W. C. Steere, Eds.), Vol. 8, pp. 237–337, Plenum, New York.
- HUEY, R. B., PIANKA, E. R., EGAN, M. E., AND COONS, L. W. 1974. Ecological shifts in sympatry: Kalahari fossorial lizards (Typhosaurus), *Ecology* **55**, 304–316.
- HUTCHINSON, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *Amer. Nat.* **95**, 145–159.
- LAWLOR, L. R., AND MAYNARD SMITH, J. 1976. The coevolution and stability of competing species, *Amer. Nat.* **110**, 70–99.
- LEÓN, J. F., AND CHARLESWORTH, B. 1978. Ecological versions of Fisher's fundamental theorem of natural selection, *Ecology* **59**, 457–464.
- LEVIN, S. A., AND UDOVIC, J. D. 1977. A mathematical model of coevolving populations. *Amer. Nat.* **111**, 657–675.
- LEVINS, R. 1968. "Evolution in Changing Environments," Princeton Univ. Press, Princeton, N. J.
- MACARTHUR, R. H. 1972. "Geographical Ecology," Harper & Row, New York.
- MACARTHUR, R. H., AND LEVINS, R. 1964. Competition, habitat selection and character displacement in a patchy environment, *Proc. Nat. Acad. Sci. USA* **51**, 1207–1210.
- MACARTHUR, R. H., AND LEVINS, R. 1967. The limiting similarity, convergence, and divergence of coexisting species. *Amer. Nat.* **101**, 377–385.
- MACARTHUR, R. H., AND WILSON, E. O. 1967. "The Theory of Island Biogeography," Princeton Univ. Press, Princeton, N. J.
- MAYNARD SMITH, J. 1978. Optimization theory in evolution, *Ann. Rev. Ecol. Syst.* **9**, 31–56.
- MAYNARD SMITH, J. 1982. "Evolution and the Theory of Games," Cambridge Univ. Press, Cambridge.
- MENDEL, B. K. 1971. On the ecological significance of Bergmann's rule, *Ecology* **52**, 845–854.
- PIANKA, E. R. 1973. The structure of lizard communities, *Ann. Rev. Ecol. Syst.* **4**, 53–74.
- PIANKA, E. R. 1974. "Evolutionary Ecology," Harper & Row, New York.
- ROUGHGARDEN, J. D. 1976. Resource partitioning among competing species—A coevolutionary approach, *Theor. Popul. Biol.* **9**, 388–424.

- ROUGHGARDEN, J. D. 1979. "Theory of Population Genetics and Evolutionary Ecology," Macmillan Co., New York.
- SCHOENER, T. W. 1969. Optimal size and specialization in constant and fluctuating environments: An energy-time approach, pp.103-114 "Diversity and Stability in Ecological Systems," in (G. M. Woodwill and H. H. Smith, eds.), pp.103-114. Brookhaven Sympos. in Biology 22. Brookhaven Natl. Lab., Upton, N. Y.
- SCHOENER, T. W. 1970. Size patterns in West Indian Anolis lizards II. Correlations with the sizes of particular sympatric species displacement and convergence, *Amer. Nat.* **104**, 155-174.
- SLATKIN, M. 1980. Ecological character displacement, *Ecology* **61**, 163-177.
- SLATKIN, M., AND MAYNARD SMITH, J. 1979. Models of coevolution, *Quart. Rev. Biol.* **54**, 233-263.
- STENSETH, N. C. 1984. Evolutionarily stable strategies in food selection models with fitness sets, *J. Theor. Biol.* **109**, 489-499.

INTRA-SPECIFIC COMPETITION IN THE SEX COMMUNICATION
CHANNEL: A SELECTIVE FORCE IN THE EVOLUTION OF
MOTH PHEROMONES?

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ABSTRACT

A model for mate competition in moths sexually signalling with pheromones is presented. The model has four variables. N is the number of individuals of each sex per area unit. r is the length of the female odour plume as detected by a responding male. ϵ is a parameter increasing with male ability to discriminate between concentrations. $r - \epsilon$ becomes the competitive part of the female pheromone plume, i.e. the distance at which an upwind female is able to distract males from downwind plumes. Assuming a random distribution of males and females the number of matings in a generation can be calculated. Introducing a fourth parameter, B = surviving offspring of each sex from a mating, the population dynamics of the population can be described. Two special cases are analysed; 1. $\epsilon = r$, and 2. $\epsilon = 0$. In case 1 mating success increases with population density towards unity. In case 2 interference between the pheromone plumes of different females will lower the mating success at higher population densities. The stability of the communicating population decreases with increasing B and ϵ . We conclude that there should be a strong selection pressure for male ability to discriminate between odour plumes under natural circumstances and for individually distinguishable pheromone plumes.

INTRODUCTION

Most moths are entirely dependent on olfactory cues in their search for mates. The females emit pheromones in minute quantities, which still can attract male moths over long distances. The amount of pheromone per female is usually in the low nano-gram range (10^{-9} g) but females of other species might produce the same compounds in as much as microgram quantities (10^{-6} g). For instance females of the turnip moth Agrotis segetum (Schiff.) (Lepidoptera:Noctuidae) release a few nanograms of (Z)-7-dodecenyl acetate per hour as a pheromone component (Löfstedt, unpubl.), whereas female cabbage loopers Trichoplusia ni (Hübner) (Lepidoptera:Noctuidae) emit the same compound in microgram quantities (Bjostad et al 1984). Thus the pheromone emission rate in a given moth species should not be ultimately explained by biosynthesical constraints, but rather by ecological and evolutionary pressures.

Under natural conditions pheromone plumes probably overlap significantly at high population densities, causing intra- as well as inter-specific competition in what has been labelled "the sex communication channel" (See e.g. Greenfield and Karandinos 1979). A similar situation is generated artificially for the control of pest insect populations by means of pheromones. When synthetic pheromones are released from numerous sources, this will result in reduced reproductive success, probably due to interference between calling females and the synthetic pheromone sources (e.g. Cardé 1976).

In the present paper a model for intraspecific competition in the moth sex pheromone communication channel is presented and its ecological and evolutionary implications are discussed. Ecologically it implies a mechanism for population regulation by self induced confusion. In an evolutionary perspective we consider reduced mating success as a result of intra-specific pheromone plume overlap, a selective force moulding the characteristics of the moth pheromone communication system.

A background to the model

Field experiments by Wall and Perry (1978, 1981) with synthetic pea moth Cydia nigricana(F.) (Lepidoptera; Tortricidae) pheromone demonstrated that under certain conditions, upwind traps can outcompete downwind ones. We observed the behavioural response of male Yponomeuta cagnagellus to overlapping pheromone plumes in a laboratory flight tunnel. The experiments were performed in a 2.5 m long x 0.9 m high x 0.9 m broad plexiglas flight tunnel operating like the one described by Miller & Roelofs (1978). Rubber septa (red 5x9 mm, Arthur H. Thomas, Co, U.S.A.) impregnated with pheromone in 100 μ l hexane were used as dispensers. A pinned male moth was attached as a female attrap. The first bait in a series was placed 1 m upwind from the point where males were released and the second bait (when present) another meter further upwind.

For the test a male moth was transferred to a metal screen release cone. The males were then exposed to pheromone by holding the cage in the plume. Males were allowed two minutes to respond and were scored for the following behaviours: upwind anemotactic flight, landing on the first bait, passing the first bait and landing on the second, and landing on the first bait but continuing to and landing on the second.

When a pheromone source equal to the first one was placed upwind, a majority of the males continued upwind without visiting the first source. When the concentration of the second source was 1/3 of the first most of the males stopped at the first source with the higher release rate, but still a significant proportion continued upwind (Table 1). Our interpretation is that an upwind female is indeed able to attract a significant number of males initiating their upwind flight to more downwind ones, and that this ability depends on the female's pheromone release rate.

Table 1. Behavioural responses of male Y.cagnagellus to overlapping pheromone plumes in a flight tunnel

Stimulus (μg) ¹		N	Upwind flight ²	Landing(%) ⁴		Continuing to 2nd bait	
1st bait	2nd bait			1st bait the	2nd bait	after visit to	
			%			1st	%
100	-	18	61	82	-	-	-
100	100	25	56	14	71		7
100	30	23	48	73	18		27

1) Mixture of Z11-14:OAc, E11-14:OAc and 14:OAc (100/3/37)

Baits assigned on their content of Z11-14:OAc

2) % of males tested

3) % of males flying upwind

The model

Consider a population of moths with an equal sex ratio and let each sex have on the average N individuals per area unit. Assume further that both sexes are randomly distributed over an infinite area. Each female emits pheromone into a plume, which due to shifting wind-fields, sweeps over an area with a geometry which we prefer to describe as a circle sector in order to make the model tractable for mathematical analysis. For simplicity this circle sector is considered the plume in the following. Let all plumes have the angle Θ in radians and the length r which is assumed to be the maximum distance over which it is possible for a male to perceive pheromone from a female and initiate upwind flight (Fig. 1). r is a variable dependent on the female emission rate (Q) and the male behavioural threshold (K) in each interaction between individual females and males.

The part of each plume in which the concentration of pheromone is above the males' perception threshold covers an area of Θr^2 square units. The average plume thus contains $\Theta r^2 N$ males and as many females.

Let the actual number of males (or females) be X , which from the assumption of random distribution is a stochastic variable distributed according to the Poisson distribution. The probability of finding a certain number of males (or females) $X = x$ thus can be calculated by (Pielou 1977, p. 116)

$$\text{Prob } (X=x) = \frac{(\Theta r^2 N)^x e^{-\Theta r^2 N}}{x!} \quad (1)$$

For the present treatment we have only need for the probabilities for finding no moths and at least one in a given plume. That is the probability that $X=0$ and $X>1$; from Eq. 1 we get

$$\text{Prob } (x=0) = e^{-\Theta r^{2N}} \quad \text{and,} \quad (2a)$$

$$\text{Prob } (x>1) = 1 - e^{-\Theta r^{2N}} \quad (2b)$$

Under certain, admittedly simplified, conditions it is possible to calculate the mating success of a given female by means of Eqs. (2a-b). Assume that both males and females mate only once, and that the latter are strictly stationary, whereas the former move upwind as long as they perceive the odour cue from a female. This would mean that females with other females upwind within a certain distance never became mated. However, from laboratory experiments (Willis & Baker 1984) it is known that male moths can distinguish a superimposed plume from a diffuse cloud of pheromone. Thus males in nature should be able to stick to a more concentrated plume if the distance to an additional upwind source is large enough. Then an upwind female can outcompete a downwind female only if she is relatively close to her competitor or if she is emitting substantially more pheromone. We define the competitive distance as $(r - \epsilon)$ (Fig. 1). ϵ could be regarded as a measure of the males ability to perceive odour concentration differences. The probability of finding no female within this distance is $e^{-\Theta(r-\epsilon)^{2N}}$. The mating success of a given female is obtained by considering those configurations of pheromone plumes that lead to mating and calculating the corresponding probabilities of their occurrence.

Mating will take place if the female is not situated in the competitive part of the plume of an upwind female (Fig. 2) and if at least one male enters her own plume, of which the respective probabilities are $e^{-\Theta(r-\epsilon)^{2N}}$ and $1 - e^{-\Theta r^{2N}}$. The probability that this specific configuration will occur is then $1 - e^{-\Theta(r-\epsilon)^{2N}} (1 - e^{-\Theta r^{2N}})$. More generally, a female will become mated whenever she is the last one in a row of i other females, of which the most downwind one has at least one male in her plume (defining the beginning of the row). This occurs, from the point of view of any given female, when: (1) she is not included in the competitive part of another female's plume $e^{-\Theta(r-\epsilon)^{2N}}$ (2) when i females have no males in their plume the probability for this is $(e^{-\Theta r^{2N}})^i$ (3) but instead have at least one

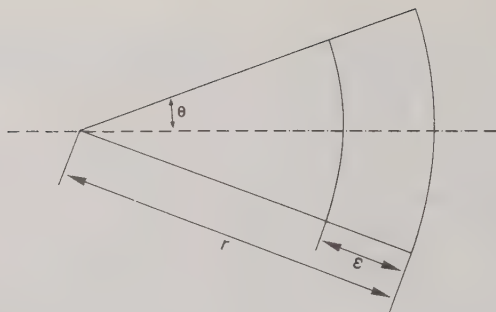


Figure 1. The assumed geometry of moth pheromone plumes. r is the size of the plume, or strictly speaking the part of the plume, with pheromone concentration above the male's perception threshold, θ is half the angle of the circle sector, and ϵ is the part of the plume with such low pheromone concentration that a denser plume superimposed on this area will be recognised by a male and prevent further upwind flight by attraction to its source.

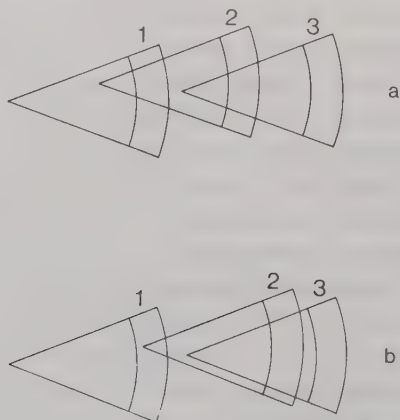


Figure 2. Models of overlapping pheromone plumes. Males entering a pheromone plume are assumed to fly upwind, as long as the pheromone concentration exceeds their behavioural threshold. In case a) female 2 is situated within the competitive part of the plume of female 1, the latter female will attract also those males that initially were attracted by female 2 and 3. In case b, female 1 will only attract those males that happens to be in her own plume, whereas female 2 attracts those that occur in both her own and the plume of female 3.

female each in the competitive parts of their plumes $(1 - e^{-\Theta(r-\epsilon)^2 N})^i$ and finally when, ⁽⁴⁾ the most downwind female has at least one male in its plume $(1 - e^{-\Theta r^2 N})$. Given that these events are independent (which they are given random distribution) this configuration will arise with the probability:

$$e^{-\Theta(r-\epsilon)^2 N} (1 - e^{-\Theta r^2 N}) (e^{-\Theta r^2 N})^i (1 - e^{-\Theta(r-\epsilon)^2 N})^i$$

The sequence of configurations obtained for $i = 0, 1, 2, \dots$ constitutes the set of mutually exclusive events that will lead to mating. The mating success $F(N)$ of any female is given as the sum of the expected probabilities of these events:

$$F(N) = e^{-\Theta(r-\epsilon)^2 N} (1 - e^{-\Theta r^2 N}) \sum_{i=0}^{\infty} (e^{-\Theta r^2 N})^i (1 - e^{-\Theta(r-\epsilon)^2 N})^i \quad (4) \quad \text{or}$$

by developing the sum

$$F(N) = \frac{e^{-\Theta(r-\epsilon)^2 N} (1 - e^{-\Theta r^2 N})}{1 - e^{-\Theta r^2 N} (1 - e^{-\Theta(r-\epsilon)^2 N})} \quad (5)$$

The number of females mating a particular season is then given by $NF(N)$, and assuming that the expected number of surviving offspring of each sex from a mating is B we obtain the following first order recurrence relation describing the change in population density between successive years $N_{t+1} = N_t BF(N_t)$, or

$$N_{t+1} = \frac{N_t B e^{-\Theta(r-\epsilon)^2 N_t} (1 - e^{-\Theta r^2 N_t})}{1 - e^{-\Theta r^2 N_t} (1 - e^{-\Theta(r-\epsilon)^2 N_t})} \quad (6)$$

This function is plotted in Fig. 3 for two sets of r , ϵ and B , together with examples of how N may change over time.

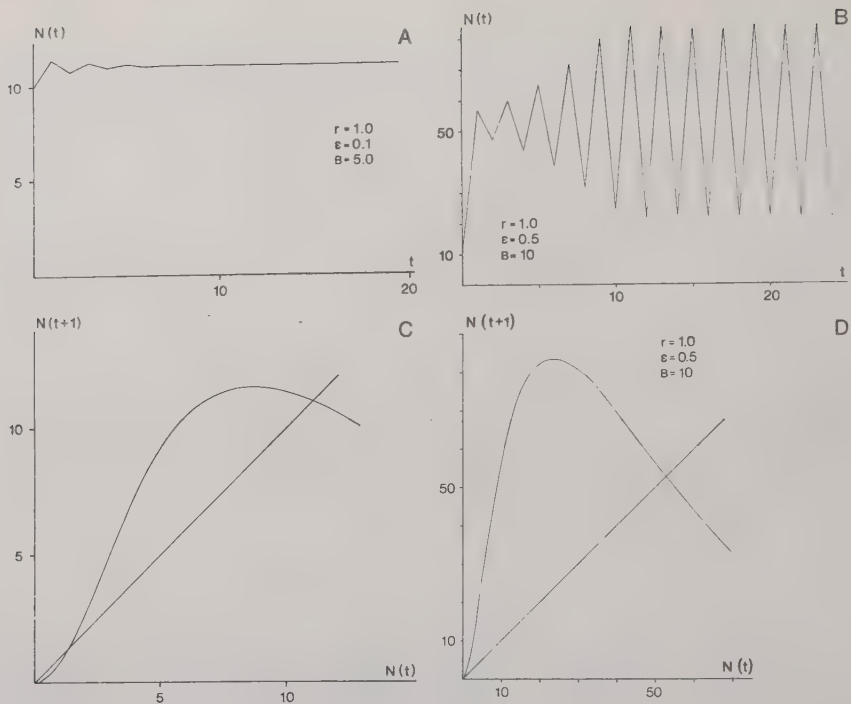


Figure 3. The model may generate a multitude of dynamic behaviours, including stable points (a), periodic (b) fluctuations and chaos depending on assumed male behavioural thresholds (r and ϵ , see text) and the number of offspring per mating (B). (c) and (d) show the function corresponding to the dynamics of a and b, respectively. The model's stability properties are analysed further in the text.

Analysis of two special cases

The equilibria of the model (Eq. 6) can be found either analytically by setting $N=N_{t+1}=N_t$ and solving the equation $N=BNF(N)$, or graphically by plotting N_{t+1} as a function of N_t as the points of intersection of the resulting graph with a 45° line through the origin (May, 1976). The only root of the equation that can be obtained analytically is the trivial $N_0=0$. The remaining equation $F(N)=1/B$ is not generally soluble. Two special cases exist, however, for which it is possible to give an analytical expression for the equilibrium densities. The cases are (i) $\epsilon=r$ and (ii) $\epsilon=0$ (see Table 2).

We have investigated the neighbourhood stability properties of the two special cases, whereas for the general model we have been forced to rely on numerical methods (Table 2 and Fig. 4, Fig. 5 and Fig. 6). Although the special cases are not very plausible descriptions of reality per se, they are interesting as endpoints of a continuum; case (ii) $\epsilon = 0$, means that the male moth is only capable of perceiving presence or absence of an odour cue, whereas case (i) $\epsilon = r$, means that he is able to distinguish between any concentration difference, given that the concentrations are above his threshold of perception. These two imaginary types of males will, respectively, mate with the most distant female and the nearest one. And, interestingly, they correspond to very different population dynamics patterns. In case (ii) we have, beside the trivial $N_0 = 0$, two equilibria denoted N_1 and N_2 in Table 2 of which the former is always unstable and the latter is stable when the number of surviving offspring B is within a certain interval (Fig 4). Numerical investigations of the general model shows that N_2 increases almost exponentially with ϵ , such that in the limit when $\epsilon \rightarrow r$, there is no longer any finite solution N_2 . The only remaining solution is therefore N_1 which as in case (i) is unstable for all values of B (See Fig 4).

The results from the numerical stability analysis of the general model is presented in Fig. 5. The general trend is that stability of the equilibrium point N_2 decreases when ϵ and B increase (there is no need for analysis of the influence of r on stability, as what matters is the ratio between ϵ and r). As far as B is concerned, this is the same phenomenon as the one observed in the discrete version of the logistic equation (May, 1976), which is destabilized by increasing the intrinsic rate of increase. Our main conclusion is thus that an improved male ability to perceive concentration differences makes the model more sensitive to an increase in the number of surviving offspring.

These results can also be obtained in a more heuristic way. Consider the two special cases : A female in case (i) will always find a mate if there is at least one male within the maximum communication distance. The probability for this to occur is in fact given by Eq. 2b (see also Table 2) and equals the proportion of the females that will mate. This proportion will increase with population density, and will eventually converge towards unity. Thus there is a positive feedback. In case (ii) this is not true above a certain level of the population density, above which the mating success declines owing to the interference between pheromone plumes.

Table 2. Local stability analysis of the two special cases of the model discussed in the main text. The two cases are $\epsilon=0$ (meaning that males cannot perceive any pheromone concentration differences whatsoever) and $\epsilon=r$ (meaning that the male always sticks to the most dense plume, thus mating with the nearest female).

Special case	
(i) $\epsilon=0$	(ii) $\epsilon=r$
State Equation: $N_{t+1} = N_t BF(N_t)$	
$F(N) = \frac{e^{-\Theta r^2 N} (1 - e^{-\Theta r^2 N})}{1 - e^{-\Theta r^2 N} (1 - e^{-\Theta r^2 N})}$	$F(N) = 1 - e^{-\Theta r^2 N}$
Equilibrium Points $\hat{N}_i$	$\hat{N}_0 = 0$
$\hat{N}_1 = -\frac{1}{\Theta r^2} \ln \left[\frac{1}{2} \left(1 + \sqrt{\frac{B-3}{B+1}} \right) \right]$	$\hat{N}_1 = -\frac{1}{\Theta r^2} \ln \left(1 - \frac{1}{B} \right)$
$\hat{N}_2 = -\frac{1}{\Theta r^2} \ln \left[\frac{1}{2} \left(1 - \sqrt{\frac{B-3}{B+1}} \right) \right]$	-

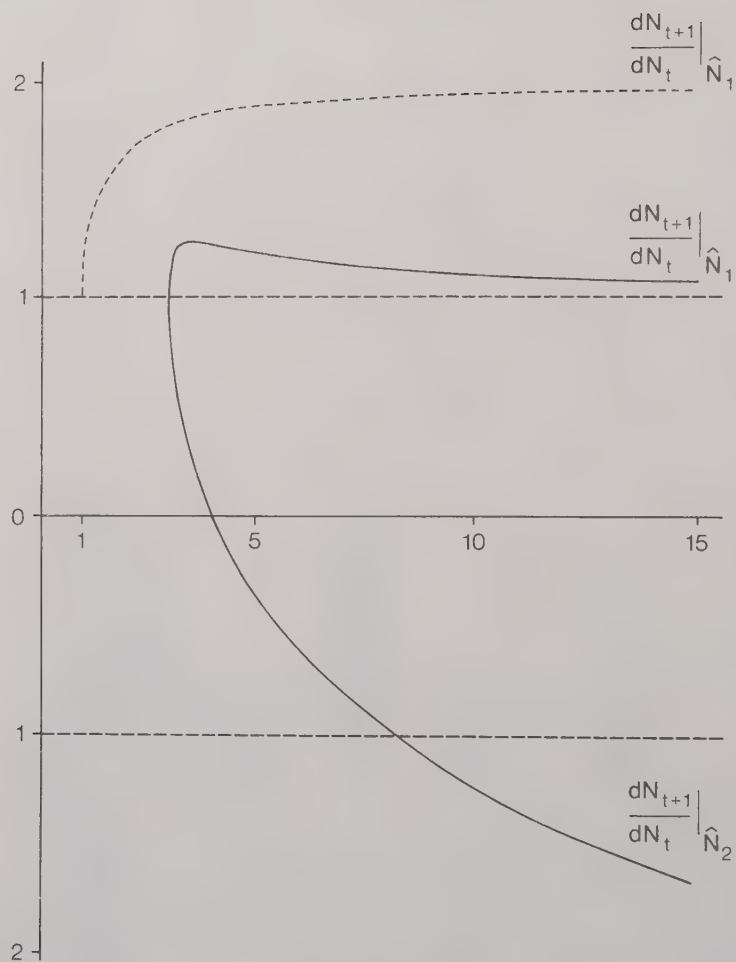


Figure 4. The derivative dN_{t+1}/dN_t evaluated for the case $\epsilon = 0$ (no male ability to discriminate between pheromone concentration solid curves) for the equilibrium point N_1 and N_2 (for the notation see the text) and for the case $\epsilon = r$ (infinite male concentration discrimination dashed curve) for the equilibrium point N_1 . In neither case N_1 is stable, whereas N_2 is stable for $\epsilon = 0$ in the interval $3 < B < 8.3$, in which $-1 < dN_{t+1}/dN_t|_{N_2} < 1$

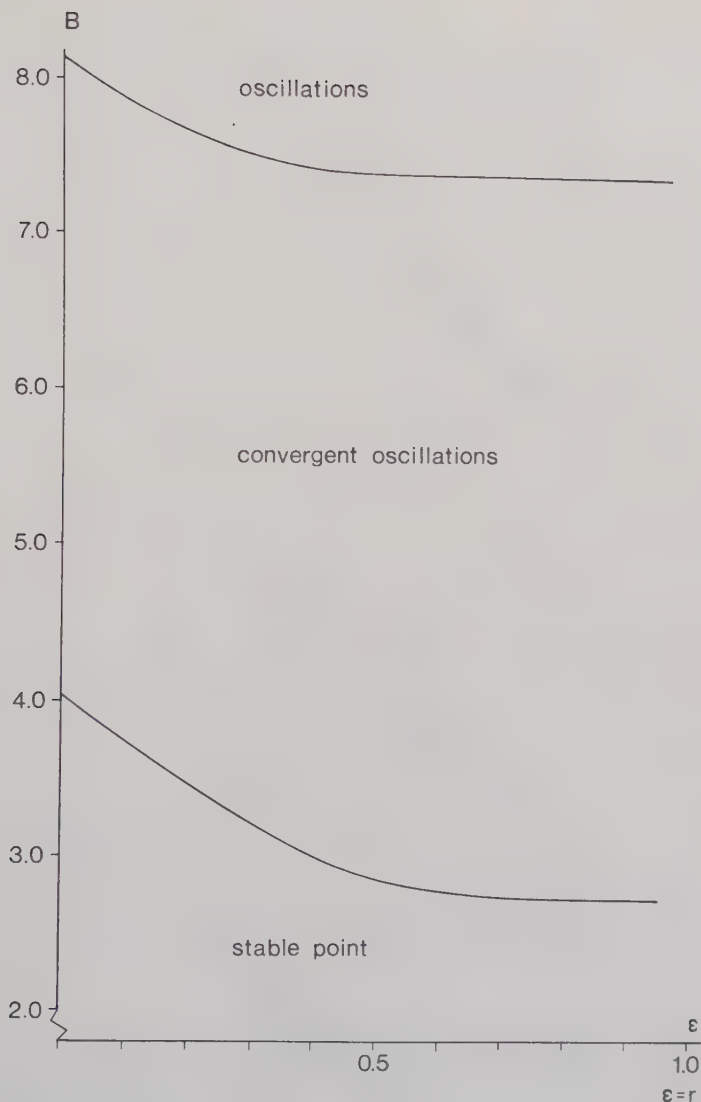
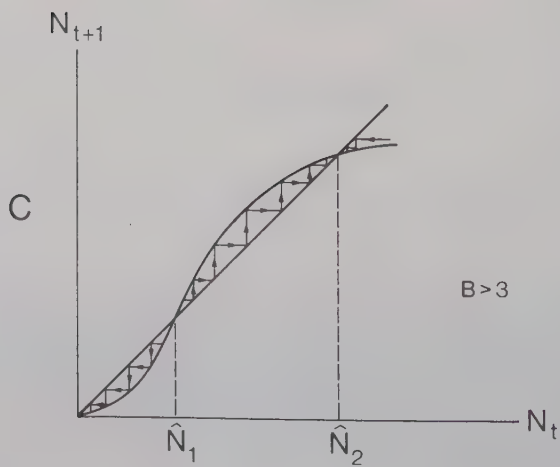
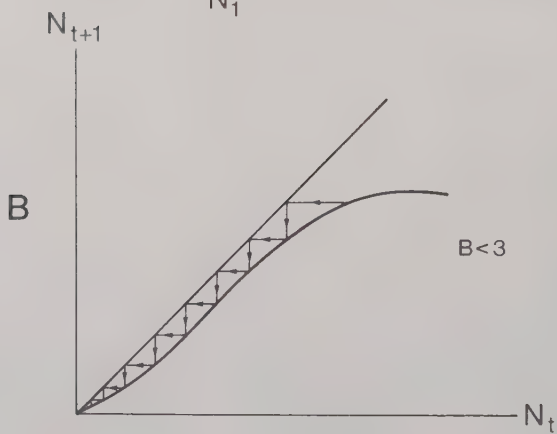
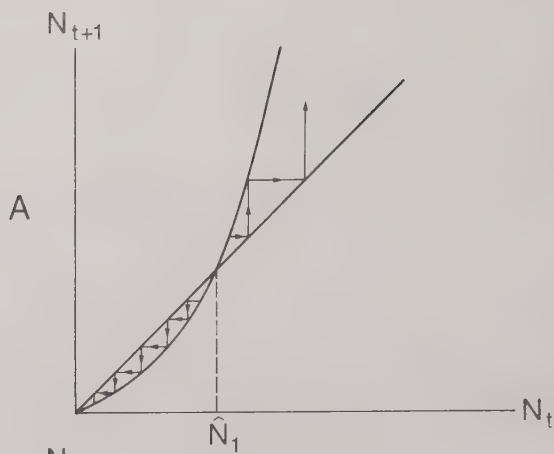


Figure 5. Stability analysis of the model. The diagram combines values of ϵ and B that correspond to asymptotic stability, convergent oscillations and cyclic behaviour. The curves were obtained by solving the equations $\frac{dN_{t+1}}{dN_t} = -1$ (upper curve) and $\frac{dN_{t+1}}{dN_t} = 0$ (lower curve) for B given by an iterative method. For each cycle in the iterations the equation $1 = BF(N)$ was solved numerically. The stability of the model decreases with increasing ϵ and B .



DISCUSSION

This paper addresses the question of the evolutionary stability of the pheromone communication system. Greenfield(1981) argued that females with low emission rates are selected for, as they will mate with the most sensitive males; their sons will be at a selective advantage in future generations, especially when the population density is low. If competition between females occur as outlined in our model, this strategy seems dangerous to us. First, a male with a higher sensitivity than average would certainly be a good mate choice at relatively low population densities, whereas this might not be true at higher ones. What counts seems to be the ability to follow a plume rather than to detect it. Second, a female with a higher-than-average emission rate will presumably attract males from larger distance (which might mean more viable males, being able of flying for long) and also more of them as their plumes cover larger areas. Thus, there should - in this respect - be a selection for higher release rates. From this we conclude that at any given density and emission rate there should rather be an optimal sensitivity. This strategy is not equal to maximal sensitivity as argued by Greenfield, but the males should evolve towards that sensitivity level, which maximizes the males resolution of calling females' pheromone plumes. If the females' emission rates increase over evolutionary time, then their sensitivity must decrease. However our model does not explain why there is not an evolutionary race between females to emit more and more pheromone. To deal with this problem the model has to be modified to allow for individual variation in female emission rates.

In addition to the quantitative aspect of moth pheromones one may recognise a qualitative one. The pheromone of a species has to be specific to ensure reproductive isolation, but individual variation in composition between females within a population is documented (e.g. Löfstedt et al. 1985).

Figure 6. The dynamic consequences of the two special cases mentioned in the text. (A) For case (i) ($\epsilon=r$) there exists just the unstable equilibrium point N_1 . This means that for initial population densities less than that value, the population will decrease, and eventually go extinct, whereas if the density is above N_1 to begin with, the population will increase exponentially. (B) For case (ii) ($\epsilon=0$) two possibilities arise: First, for $B<3$ the only equilibrium is $N_0=0$ and for whatever the initial population density might be, the population will go to extinction. Secondly, for $B>3$, all three equilibria exists (N_0 , N_1 and N_2 , see text). Given that $B<8.3$ the population will approach the last point if the population is greater than N_1 to begin with. These two possibilities exist for any value of $\epsilon<r$, i.e., there is a critical value of B , below which $N_0=0$ is the only existing equilibrium. This critical threshold in B decreases with ϵ and converges towards one when $\epsilon \rightarrow r$.

Although no evidence is available, it is tempting to speculate that if these differences are heritable - and perceivable by the males - they might increase the males' ability to resolve pheromone plumes and get mated.

In populations with a heritable variation in female pheromone production (Q) and male sensitivity (K), natural selection will act on these traits in a density - as well as frequency - dependent manner. Sower et al (1971) suggested that in areas of high moth population densities a high ratio would perhaps be a liability, resulting in many males responding to pheromone from an upwind female that has already started copulation with a male originally near her. At low population densities, pairs with a high Q/K ratio would have a much better chance of mating. In conclusion they speculate that a variable Q/K ratio within a population may be a biological asset. However, this group selectionist argument does not seem necessary as it is obvious from our model that population fluctuations and natural selection at the level of the individual will maintain some variation in these characters.

Our model assumes a mechanism for reduced mating at high population densities that is different from the one suggested by Sower et al. (1971). However this does not mean any principal difference and the mechanisms could very well be combined; the selective pressures and the possible impact on population dynamics remain the same.

The possibility of population regulation by competition between pheromone plumes is speculative and has to be critically tested. West-Eberhardt (1984) points out that it is not clear to what degree sexual calling of females should really be considered "competitive". Whereas calling males certainly compete for females, it is not known to what degree females engage in calling contests with other females. Two "competitive" causes for the evolution of female calling are put forward, which justify our model; 1) the advantage of attracting more than one male, allowing comparison of potential mates, and 2) mutual sexual selection, in which due to some kind of parental investment by males, both males and females compete for mates. Our model - of course - applies to both situations. Unfortunately we know hardly anything about how competition between female pheromone plumes effect the mate seeking behaviour of males under natural circumstances. The field experiments by Wall and Perry (1978, 1981) with synthetic pheromone sources demonstrated that under certain conditions upwind traps could outcompete downwind ones. Under natural conditions males will not get "trapped" by females if they do not get a mate, but they will continue searching for unmated females as in our flight tunnel experiment. In a similar way downwind females will continue calling until they most probably end up mated

after a prolonged period of calling. However, this extra cost for finding a mate will be subject to selection as well as the prolonged male searching time. It seems important to us to design field experiments like the one performed by David et al. (1983), where male attraction to pheromone is studied in the field. The use of multiple pheromone sources in shifting wind-fields, will through light on the nature of pheromone plume interactions under natural circumstances.

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REFERENCES

- Bjostad, L.B., Linn, C.E., Du, J.-W., and Roelofs, W.L. (1984). J. Chem. Ecol. 10, 1309.
- Cardé, R.T. 1976. Environ. Health Perspect. 14, 133.
- David, C.T., Kennedy, J.S., and Ludlow, A.R. (1983). Nature 303,804.
- Greenfield, M.D. (1981). Florida Entomologist 64, 4.
- Greenfield M.D. and Karandinos, M.G. (1979). Ecological Monographs 49, 403.
- Löfstedt, C., Lanne, B.S., Löfqvist, J., Appelgren, M., and Bergström, G. (1985). J. Chem. Ecol. 11, 1181.
- May, R.M. 1976). Nature 261, 459.
- Miller, J.R. and Roelofs, W.L. (1978). J. Chem. Ecol. 4, 187.
- Pielou, E.C. (1977). Mathematical Ecology. New York, John Wiley & Sons.
- Sower, L.L., Gaston, L.K., and Shorey, H.H. (1971). Ann. Entomol. Soc. Amer. 64, 1448.
- Wall, C. and Perry, J.N. (1978). Ent. exp. & appl. 24, 155.
- Wall, C. and Perry, J.N. (1981). Ent. exp. & appl. 28, 313.
- West-Eberhard, M.J. (1984) in Insect Communication, T. Lewis (ed.) 58:155. pp 284-324 Academic Press, Orlando.
- Willis, M.A. and Baker, T.C. (1984). Physiological Entomology 9, 341.

The importance of egg hatchability and nest predation in clutch size evolution in altricial birds

Sigfrid Lundberg

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All the different mortality factors acting on avian offspring can roughly be divided into two groups with respect to their level of action. First, there are deaths of individual eggs and nestlings, and, second, the destruction of entire clutches. Deaths of eggs on the latter level is often due to predation and deaths on the former to infertility of the eggs or early deaths of embryos. Mortality due to starvation occur on the individual chick level, and its intensity is assumed to be correlated positively to clutch size. Therefore, there will generally exist a most productive brood size.

When egg hatchability and predation are considered together in one model three possibilities arise: (1) the optimal clutch size may equal the most productive brood, (2) *clutch size reduction* is possible when the daily risk of predation is high. It is shown that predation potentially is a more important determinant of clutch size evolution than has been generally appreciated. (3) *Compensatory egg laying* may evolve when the daily risk of predation is low. The latter adaptation is favoured by a high incidence of infertile eggs and the former by a low. An increase in food availability may lead to both outcomes, dependent on the incidence of deaths of eggs.

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Все различие факторы смертности, действующие на выводки птиц, могут грубо быть разделены на две группы по степени их воздействия. Во-первых, гибель отдельных яиц и птенцов и во-вторых, гибель целых выводков. Гибель яиц в последнем случае является результатом хищничества, а в предыдущем – результатом того, что яйца были непродуктивными, либо следствием гибели эмбрионов. Гибель от голода наблюдалась у отдельных птенцов, размеры этой смертности позитивно коррелируют с размером выводка. Таким образом вообще может существовать наиболее продуктивная величина выводка. Если рассматривать способность к вылуплению птенцов из яиц и изlayтие их хищниками вместе в одной модели, возникают три возможности: 1. оптимальный размер кладки может равным образом дать наиболее продуктивные выводки; 2. уменьшение размера кладки возможно при высокой риске ежедневного пресса хищников; показано, что хищничество – потенциально более важный детерминирующий фактор эволюции размера кладок, чем это в целом предполагалось; 3. компенсаторная откладка яиц может иметь место, если ежедневный риск хищничества низок. Последняя адаптация стимулируется при высокой встречаемости неоплодотворенных яиц, а первая – при низкой. Увеличение доступности пищи может привести к обоим следствиям, в зависимости от случаев гибели яиц.

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Introduction

Lack (1947a) claimed that clutch size is primarily determined by the amount of food available to the parents for rearing their young. He states that "the average clutch-size is ultimately determined by the average maximum number of young which the parents can successfully raise in the region and season in question" (p. 319). Assuming that the variation in clutch size is to a large extent heritable he concludes that it might be maintained as a balanced polymorphism (Lack 1947b). Although the most productive brood size not always equals the most common clutch size (see Klomp (1970) for a review) the hypothesis that young from large broods suffer a higher mortality than young from smaller ones, has been confirmed in most cases. This trend has been even more pronounced in studies where the brood size has been manipulated experimentally (Högstedt 1980, Klomp 1970, Loman 1980, Schifferli 1978). It can be argued that Lack's hypothesis, as cited above, covers all conceivable mortality factors. This was, however, not his view.

Egg mortality as a possible determinant of clutch size was rejected by him (Lack 1947b) since after omitting all complete nest failures in partridge (*Perdix perdix*), he found that the remaining mortality of individual eggs was fairly constant and independent of clutch size. Therefore, it can not act as a directional selection pressure against an increase in clutch size.

Nest predation might also regulate the clutch size especially in tropical areas (Skutch 1949). The risk of nest predation increases with increasing clutch size, because the amount of time a nest is exposed to predators is dependent on the number of eggs it contains, and the frequency of feeding visits is a function of the number of nestlings. However, Lack felt that his mechanism requires an unrealistically high predation rate in order to work.

The possibility that birds might have evolved compensatory egg laying in order to compensate for losses during incubation lies implicit in Lack's hypothesis. Although it is an old idea, it has not been seriously considered neither by Lack himself nor by any later worker. The reason for this is probably that the overwhelming problem has been what factors are *limiting* the clutch size. The importance of predation in clutch size evolution is, however, still under dispute; some authors (e.g., Klomp 1970 and Ricklefs 1977) adhere to the tenet that it is negligible, whereas others (e.g., Perrins 1977) maintain that predation might modify clutch size under certain circumstances, albeit these are rare.

The question I am addressing in the present papers is: Given that Lack was basically correct, that food shortage is the most important factor in the evolutionary determination of clutch size, what is the impact of the other two, egg hatchability and predation?

The model

The reproductive output of birds is determined by several kinds of mortality factors, acting on two levels: First, eradication of entire clutches, which is assumed to be mainly due to predation, bad weather and the like; mortality of this kind can be described as a constant risk exponentiation per unit time and the overall survival is then correlated to the clutch size since the duration of the nesting period depends on the clutch. Secondly, death of individual offspring, on the egg stage due to low hatchability and on the nestling period to starvation.

The question asked is: When is it advantageous to alter clutch size for some other reason than starvation, given that this factor is the limiting one to begin with? The rationale for this procedure is that starvation and other related factors seem to be the most widely accepted clutch-size limiting factors in the literature (e.g., Lack 1947a, Klomp 1970, Perrins 1977, Ricklefs 1977).

Thus, let the survival of chicks *within nests* be a decreasing function of the brood size x . (Note the usage of clutch and brood size as, respectively, the number of eggs laid and the number of eggs that hatch). For mathematical purposes I will assume that the survival $f(x)$ of chicks in broods of size x is a linear function $f(x) = 1 - x/2K$, whenever the specification of a function is needed. The reproductive output is then $xf(x) = x(1 - x/2K)$, giving a most productive brood size K , which does not necessarily be an integer.

The effect of food shortage and mortality of individual eggs

Consider a phenotype paying N eggs. Let each egg face a probability of death p . Hence, x , the number of hatchlings from a clutch with N eggs, is a stochastic variable. We can describe the hatching as N independent trials,

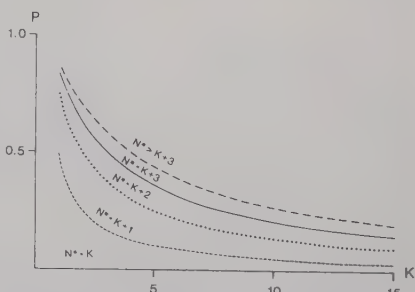


Fig. 1. Graphic interpretation of the conditions Eqs 5 of optimality of any given clutch size as a function of p , the frequency of unhatched eggs, and K , the most productive brood size. In the area below the dashed graph the optimum clutch-size is $N^* = K$ for any combination of K and p , whereas in the area between dashed and dotted graphs, the optimum clutch-size is $N^* = K + 1$; and so forth.

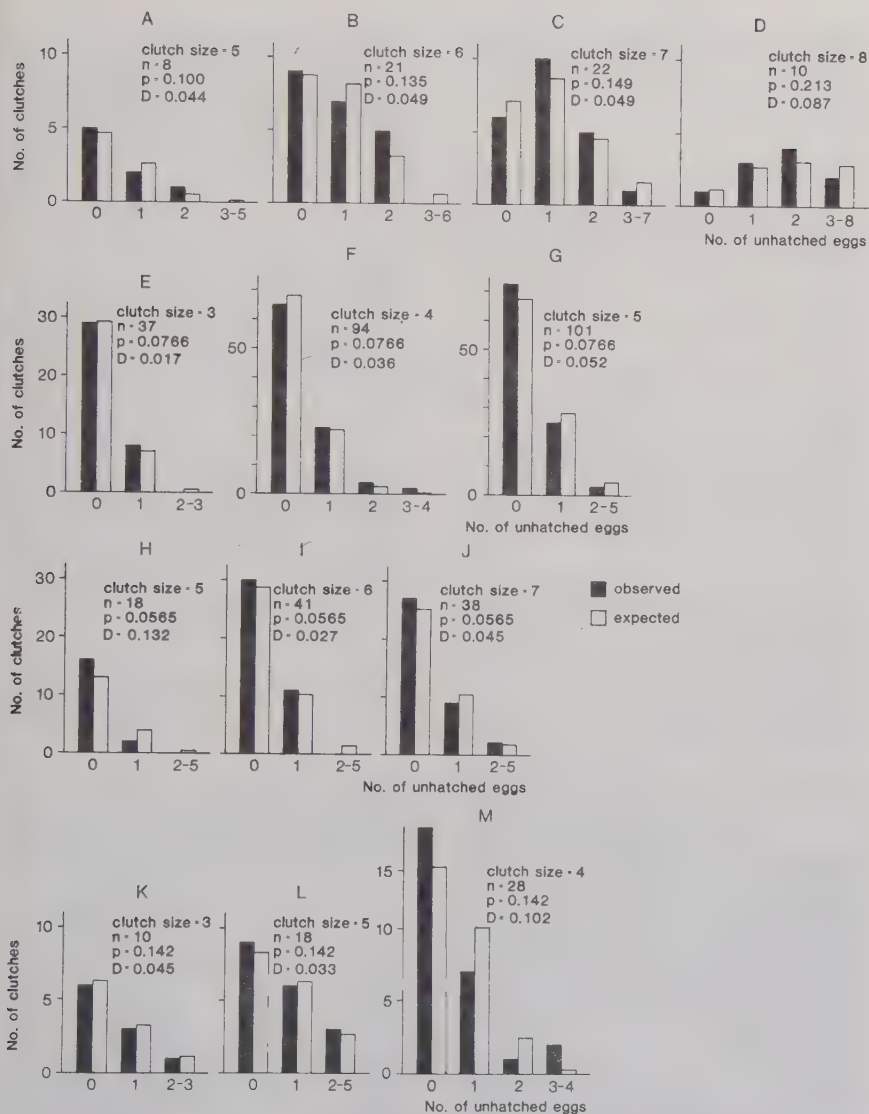


Fig. 2. The distribution of clutches with different number of unhatched eggs for four bird species: magpie (*Pica pica*) A-D, hooded crow (*Corvus corone*) E-G, pied flycatcher (*Ficedula hypoleuca*) H-J and yellow-billed shrike (*Corvinella corvinus*) K-M. References as in Tab. 1. The open bar is the expected binomial distribution. The same frequency of unhatched eggs (p) was used for calculating the expected distributions for all clutch-sizes in those species where there is no significant correlation between clutch-size and p. The goodness of fit was tested by means of the Kolmogoroff-Smirnoff one-sample test. The D-statistics are given in the figure; no significant deviation was found from the expected ($P > 0.20$ in all cases).

each with a probability of success (a healthy hatchling) $1-p$. x is thus distributed according to the binomial distribution. It follows that the proportion $P(x, N)$ of nests that originally contained N eggs of which x hatches is given by

$$P(x, N) = \binom{N}{x} (1-p)^x p^{N-x} \quad (1)$$

In order to obtain the expected production of fledglings from nests that originally contained N eggs, R_N , we must calculate the binomial expectancy of the function $xf(x)$:

$$R_N = \sum_{x=0}^N x(1-x/2K)P(x, N) \quad (2)$$

Since the binomial expectancies of x and x^2 are $N(1-p)$ and $N(N-1)(1-p)^2 + N(1-p)$ (Ross 1972) Eq. 2 reduces to

$$R_N = N(1-p) - (N(N-1)(1-p)^2 + N(1-p))/2K \quad (3)$$

The optimum clutch size N^* is defined as

$$R_{N^*} = \max_N (R_N) \quad (4)$$

At optimum the inequalities $R_{N^*} > R_{N^*-1}$, and $R_{N^*} > R_{N^*+1}$ are fulfilled.

By using them and Eq. 3 we get that $N = N^*$ when p lies between the interval

$$\frac{2(N-K)-1}{2(N-1)} < p < \frac{2(N-K)+1}{2N} \quad (5)$$

Eq. 5 is interpreted graphically in Fig. 1.

This result hinges on two fundamental assumptions, the first of which is that the number of unhatched eggs within clutches is distributed according to the binomial distribution. I have fitted the number of unhatched eggs to this distribution for four bird species (Fig. 2). There was in neither case any significant deviation from the expected distribution. The biologically most plausible deviation is a contagious distribution, which would mean that relatively few clutches contribute with a large number of unhatched eggs. There seem to be some tendencies in this direction in yellow-billed shrike (*Corvinella corvina*) (See Fig. 2).

The second assumption, which I regard as less critical, is that the incidence of unhatched eggs are independent of clutch size. This is true for partridge (*Perdix perdix*) (Lack 1947b), hooded crow (*Corvus corone*), pied flycatcher (*Ficedula hypoleuca*) and great tit (*Parus major*). If there is any correlation between p and clutch size one would expect that it should be positive. This is so for magpie (*Pica pica*) and tufted duck and scaup (*Athya fuligula* and *A. marila*). However, I have found one species, savannah sparrow (*Passerculus sandwichiensis*) for which the opposite is true. References and further details concerning these data are given in Tab. 1. In the case of tufted duck and scaup the strong correlation is presumably a result of intraspecific nest parasitism. The parasitic eggs are often laid after that the incubation has commenced; therefore, their hatching fails more often than non-parasitic eggs.

The effect of food shortage and total nest destruction

In this section I will ignore the mortality of individual eggs and consider the joint effect of total nest failure

Tab. 1. The incidence of unhatched eggs in seven birdspecies and its correlation with clutch size.

Species	Clutch size (N) range	Incidence of unhatched eggs (p) range	Incidence of unhatched eggs (p) mean	Correlation ¹ between p and N	n	Ref
Magpie (<i>Pica pica</i>)	5-8	0.100-0.213	0.180	1.0 ($P < 0.05$)	61	Högstedt (pers.comm.)
Yellow-billed shrike (<i>Corvinella corvina</i>)	(2)3-5(6)	0.134-0.167	0.142	nd ²	56	Grimes (1980)
Great tit (<i>Parus major</i>)	2-12	0.056-0.129	0.046	-0.57 (NS)	436	Perrins (1979)
Savannah sparrow (<i>Passerculus sandwichiensis</i>)	2-5	0.046-0.125	0.067	-1.0 ($P < 0.05$)	284	Dixon (1978)
Hooded crow (<i>Corvus corone</i>)	3-6	0.063-0.098	0.079	-0.20 (NS)	248	Loman (pers.comm.)
Tufted duck (<i>Athya fuligula</i>) ³ and scaup (<i>A. marila</i>)	-	-	-	-	-	-
Pied flycatcher (<i>Ficedula hypoleuca</i>)	6-19	0.025-0.229	0.051	0.943 ($P < 0.001$)	283	Hildén (1964)
	4-8	0.022-0.050	0.042	-0.30 (NS)	67	Karlsson (pers.comm.)

Notes:

¹ Spearman rank correlation coefficient (R_s).

² Not determined, since the sample sizes for 2 and 6 egg clutches are too low for estimating p .

³ Pooled data for both species.

and food shortage. Since all eggs survive until hatching the survival rate of the nestlings is $f(N)$; we will not assume any particular function but just impose the constraints that $f'(N) < 0$ and $f''(N) \leq 0$. The production of fledglings in the absence of predation is $Nf(N)$. The most productive clutch size is then given by solving the equation $d(Nf(N))/dN = 0$. Let the solution be K as in the previous section. K is given by

$$f(K) + Kf'(K) = 0 \quad (6)$$

Let S be the probability that a nest will survive one day, then the fraction of nests that survive until fledging is $S^{N^{i-1}}$, where i is the duration of the nestling and incubation periods and it is assumed that the female lays one egg a day and that the incubation commences at the day when the last egg is laid. The expected production of fledglings from a nest that originally contained N eggs is then

$$R_N = S^{N^{i-1}} Nf(N) \quad (7)$$

The most interesting question is: When is predation a sufficiently strong selection pressure for decreasing the clutch size, or more precisely: when is $N^* < K$? The answer is

$$\text{when } R_{K-1} > R_K \text{ or} \\ KS^{K+i-1} f(K) < (K-1)S^{K+i-2} f(K-1) \quad (8)$$

By rearranging we obtain

$$S < \left(1 - \frac{1}{K}\right) \frac{f(K-1)}{f(K)} \quad (9)$$

Now, we imposed the constraint that $f''(K) \leq 0$, i.e., that f is concave or linear. Under this assumption we have $f(K-1) - f(K) \leq f'(K)((K-1) - K)$ or by rearranging we obtain

$$f(K-1) \leq f(K) \left(1 - \frac{f'(K)}{f(K)}\right), \quad (10)$$

but by using Eq. 6 we have that

$$f(K-1) \leq f(K) \left(1 + \frac{1}{K}\right) \quad (11)$$

The equality holds when f is a linear function. By combining Eqs 9 and 11 we get

$$S < \left(1 - \frac{1}{K}\right) \frac{f(K-1)}{f(K)} < \left(1 - \frac{1}{K}\right) \left(1 + \frac{1}{K}\right). \quad (12)$$

Thus, a necessary but not sufficient condition for clutch size reduction to evolve is that

$$S < 1 - \frac{1}{K^2}. \quad (14)$$

The joint effect of food shortage, total nest destruction and losses of individual eggs

When considering the interactions between all three types of mortality factors we combine the models in the previous sections. The expected reproductive output from a nest originally containing N eggs, is given by Eq. 3.

However, only a fraction $S^{N^{i-1}}$ of the nests remains at hatching. Thus

$$R_N = S^{N^{i-1}} ((1-p)N - ((1-p)^2 N(N-1) + N(1-p)) / 2K) \quad (15)$$

The optimum clutch size, N^* , is again found by applying Eq. 4, but we will confine our analysis to searching a condition of optimality of the strategy to lay exactly the number of eggs that corresponds to the most productive brood size. $N^* = K$ is optimal when p lies within the interval

$$1 - \frac{(K-S(K+1))(2K-1)}{K(K-S(K+1)-1)} > p > 1 - \frac{(K(1-S)-1)(2K-1)}{(K-1)(K(1-S)-2)}. \quad (16)$$

Hence this model combines the outcomes of the two previous ones: both clutch size reduction and compensatory egg laying are possible. Eq. 16 is interpreted graphically in Fig. 3.

Discussion and conclusions

The effect of food shortage and egg hatchability

When predation is absent, the only possible outcomes are $N^* = K$, i.e., exact correspondence between optimum clutch size and the most productive brood size, or $N^* > K$, i.e. evolution of compensatory egg laying. This occurs whenever the incidence of infertile eggs exceeds a certain level (Fig. 1). Alternatively we can say, in terms of the number of successfully hatched eggs (on average $((1-p)N)$), that when the number of hatchlings is less than

$$\left[1 - \frac{2(N-K)+1}{2N}\right] N = K - \frac{1}{2} \quad (17)$$

it pays to evolve compensatory egg laying. This explains the shape of the curves in Fig. 1; in small clutches the

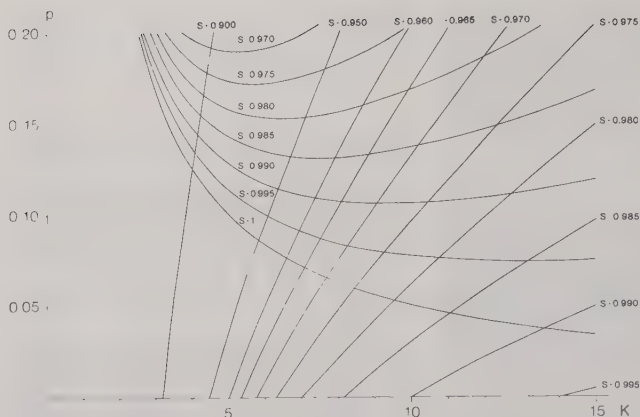


Fig. 3. Graphic interpretation of Eqs 16. These graphs predict the optimum clutch-size (N^*) given that data on the daily survival rate of the nests (S), the frequency of unhatched eggs (p) and the most productive brood size are known. For each value of S there are two graphs, and the area between them describes the combinations of K and p that give $N^* = K$; combinations above the upper curve (corresponding to the first inequality in Eq. 16) give $N^* > K$ and those below the lower (corresponding to the second) $N^* < K$.

mortality must increase substantially before the number of surviving eggs is less than $K - 1/2$, whereas in larger a much smaller increase is needed.

If compensatory egg laying is a real phenomenon, then how can it be detected? In species with adaptive variation in clutch size, e.g. magpie (*Pica pica*) (Högestedt 1980) and red-winged blackbird (*Agelaius phoeniceus*) (Shipley and Fretwell 1982), compensatory egg laying may lead to a bimodal distribution of clutch sizes. For example, consider a species that on average lays 10% infertile eggs, then according to Fig. 1 it may pay for this species to lay one additional egg in habitats where 5 or more nestlings can be successfully raised. Hence, if there in an area exist habitats with most productive brood sizes of 3, 4, 5 and 6 hatchlings, then the optimal clutch sizes in the respective habitats would be 3, 4, 6 and 7 eggs. As far as I know, bimodal clutch size distributions within restricted areas have never been reported. There are, however, several cases reported where the clutch size varies between regions, e.g., between mainland and islands (Lack 1947a) and compensatory egg-laying may be one of the factors which cause such phenomena.

Another way of detecting compensatory egg-laying is to search for species in which the most common clutch size is larger than the most productive brood size. However, this seems to be rare among birds (Klomp 1970). One case is the common heron (*Ardea cinerea*) (Owen 1960). Unfortunately Owen does not give the percentage unhatched eggs, but he mentions that "the brood size was not always the same as the clutch size as there were often some eggs that failed to hatch".

It may be possible to resolve experimentally whether or not a given species with a high incidence of infertile eggs really compensates for expected losses during in-

cubation. I propose an experimental design as follows. In a series of nests within a habitat the infertile and unhatched eggs are substituted with fertile and unhatched eggs are substituted with fertile ones. Enemer and Arheimer (1980) have presented a simple technique which makes it possible to estimate the incidence of infertile eggs at an early stage of incubation. In another group of nests fertile eggs are substituted with fertile ones as a control experiment. Obviously, if the reproductive output from the latter kind of nests is less than that of the former, then the hypothesis of compensatory egg-laying is refuted.

The effect of food shortage and total nest destruction

Contrary to several other studies (e.g. Lack 1947a, Ricklefs 1977, Klomp 1970) the present model predicts that predation and other mortality factors that acts mainly on entire clutches are important in the evolutionary determination of clutch size. Lack (1947b) rejects the hypothesis that predation might be important in partridge (*Perdix perdix*) for the following reason: If predation alone should be the factor that determines clutch size the daily predation rate must be rather high, since in order to "reduce the average clutch size from, say, 16 to 15 eggs, it would be necessary for slightly more than one in sixteen nests to be destroyed on the last day of laying". Mathematically his argument can be expressed as

$$S < 1 - \frac{1}{N^*} \quad (18)$$

The prediction from the present treatment is that in a population in which the clutch size is already limited by

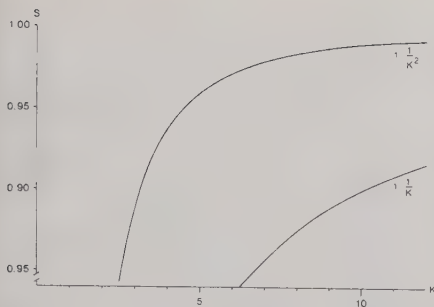


Fig. 4. Conditions for clutch-size reduction, the upper depicting Eq. 14 and the lower Eq. 18, describing when clutch-size reduction may occur for the case that food shortage and predation, respectively, are the main clutch-size limiting factors. The prediction from the present model is that clutch-size reduction never will occur above the upper curve, but is possible below it.

food shortage it may be reduced even further when $S < 1 - 1/K^2$ (Eq. 14). Note that this condition is necessary but not sufficient; the critical level under which clutch size reduction will occur, is always between Lack's condition (Eq. 18) and the one predicted by Eq. 14. Under those very general assumptions made in this model we can conclude that clutch size reduction may be more important than has been appreciated so far. Eqs 14 and 18 are depicted in Fig. 4.

The joint effect of food shortage, total nest destruction and losses of individual eggs

When the three mortality factors are considered in the same model we obtain both outcomes, clutch size reduction and compensatory egg-laying. This means that for each pair of values of the daily survival of nests (S) and the most productive brood size (K), there exists two thresholds of the incidence of unhatched eggs, between which the most productive brood equals the optimal clutch (see Eq. 16). These conditions are visualised in Fig. 3 for biologically reasonable parts of parameter space.

For really low daily survival rates, the condition for when it is advantageous to decrease clutch size below the most productive brood size is almost independent of the incidence of infertile eggs. Thus for, say, $S = 0.9$ it is never advantageous to have a clutch size less than K when K is 3 or less whatever the value of p might be, whereas in habitats with more food and accordingly higher K -values, it is always favourable to be conservative and decrease the clutch.

For species with high rates of unhatched eggs, say about 17%, we can never expect that compensatory egg-laying should evolve within species with higher daily mortality than 2.5% ($S = 0.975$). When S is in this regime it might, however, be favourable, to reduce the clutch if p is not too low. Consider the cases that $K = 7$ and $K = 9$ in Fig. 3 for $S = 0.975$. For the latter value clutch size reduction would be favoured by natural selection when p is less than 0.072 (the optimal clutch would be 8 eggs), otherwise it would be optimal to lay exactly 9 eggs. In the former case it is advantageous to lay exactly 7 eggs if p is not extremely low, i.e., less than 2%.

For still higher S -values, compensatory egg laying becomes a reasonable option. Let $S = 0.99$, say, then if p is 15% or higher, natural selection favours increase in clutch size in habitats good enough to make 4 or more chicks the most productive brood size.

One interesting feature of some of the curves describing when an increase in clutch sizes is favourable, is that they have a minimum. For instance, when $p = 0.11$ and $S = 0.99$, compensatory egg-laying is favoured by natural selection in the interval $7 < K < 12$ but not otherwise. It is also noteworthy that for high S -values, clutch size reduction can not evolve unless p are relatively small and K relatively large.

To summarize the predictions from this model, we have that clutch size reduction is possible when the daily survival rate S is low and compensatory egg-laying when it is high. The latter adaptation is expected in species with high incidence of unhatched eggs. An increase in K may favour both adaptations and the actual outcome depends on the value of p .

A few words can be said about the global trends of the parameters K , p and S : (1) The food availability, and thus K , might be higher in the temperate climate zones than in the tropical (Lack 1947a), since the amount of food the parents can bring to their young depends on the day length. (2) S might be lower in the tropics than elsewhere, since the risk of nest predation is supposed to be higher there than in temperate areas (Skutch 1949). (3) p tends to increase towards the south (Hildén 1964). This has been observed in both American and European geese species, and the cause may be that heat can start the embryogeny prematurely. When this irreversible process has started, one cool night may be enough to kill the embryo.

It is also possible to test experimentally the hypothesis of clutch size reduction. The hypothesis is readily resolved by means of an ordinary brood or ideally clutch size manipulation experiment, if the causes of deaths can be recorded in some detail. Thus, if the most productive brood, when omitting all nest failures, is less than or equal to the natural clutch size, or if it has a lower productivity than the on average most productive brood when the complete nest failures are included, or both, then the hypothesis of clutch size reduction is refuted.

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References

- Dixon, C. L. 1978. Breeding biology of the Savannah Sparrow on Kent Island. – *Auk* 95: 235–246.
- Enemar, A. and Arheimer, O. 1980. Trans-illumination of passerine bird eggs in field studies on clutch size and incubation. – *Ornis Scand.* 11: 223–227.
- Grimes, L. G. 1980. Observations of group behaviour and breeding biology of the Yellow-billed shrike *Corvinella corvina*. – *Ibis* 122: 166–197.
- Hildén, O. 1964. Ecology of Duck populations in the island group of Valassaaret, Gulf of Bothnia. – *Ann. Zool. Fenn.* 1: 153–277.
- Högstedt, G. 1980. Evolution of clutch size: Adaptive variation in relation to territory quality. *Science* 210: 1148–1150.
- Klomp, H. 1970. The determination of clutch size. A review. – *Ardea* 98: 1–124.
- Lack, D. F. 1947a. The significance of clutch size. Part I. – *Ibis* 89: 302–352.
- 1947b. The significance of clutch size in the partridge (*Perdix perdix*). – *J. Anim. Ecol.* 16: 19–25.
- Loman, J. 1980. Brood size optimization and adaptation among hooded crows *Corvus corone*. – *Ibis* 122: 494–500.
- Owen, D. F. 1960. The nestling success of the heron *Ardea cinerea* in the relation to the availability of food. – *Proc. Zool. Soc. London* 133: 597–617.
- Perrins, C. M. 1977. The role of predation in the evolution of clutch size. – In: Stonehouse, B. and Perrins, C. M. (eds), *Evolutionary ecology*. MacMillan, London.
- 1979. *British Tits*. – Collins, London.
- Ricklefs, R. E. 1977. A note on the evolution of clutch size in altricial birds. In: Stonehouse, B. and Perrins, C. M. (eds), *Evolutionary ecology*. MacMillan, London.
- Ross, S. M. 1972. *Introduction to probability models*. – Academic Press, New York.
- Schifferli, L. 1978. Experimental modification of brood size among house sparrows *Passer domesticus*. – *Ibis* 120: 365–369.
- Shiple, F. S. and Fretwell, S. D. 1982. A test for adaptive intraspecific clutch variability in red-winged blackbirds (Manuscript).
- Skutch, A. F. 1949. Do tropical birds raise as many young as they can nourish? – *Ibis* 100: 1–30.

ON REPRODUCTIVE SUCCESS, ITS EVOLUTIONARY REGULATION
AND VARIATION WITHIN AND BETWEEN SPECIES

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ABSTRACT

The question how reproductive success is regulated evolutionarily when clutch size is under natural selection is discussed under the assumption that what is maximized is the expected number of offspring produced each breeding occasion. The major selective force is assumed to be the mortality of the young.

Two general models are considered, the first of which take into account an arbitrary number of clutch size dependent mortality factors. It is shown that one of them is always a limiting factor in the sense that the optimal clutch size is always less than that clutch that would have evolved if this very factor had been the only affecting the outcome of the breeding. Further, the survival at optimum is shown to be a mean value of those that should have evolved if each factor were allowed to act in isolation.

The second model involves demographic stochasticity, making it possible to predict the entire distribution of outcomes of breeding in addition to mean reproductive output, survival, and clutch size at optimum.

Finally, it is shown the presence of a mortality factor which clutch size dependence is "multiplicative" (i.e., the fraction that escapes its action can be described as S^x , where S is a positive constant $0 < S < 1$ and x is clutch size), leads to the convergence of reproductive success towards e^{-1} (= 37 %) under some restricted but still realistic conditions.

INTRODUCTION

One of the basic tenets in avian breeding biology is Lack's (1947) hypothesis for the evolutionary determination of clutch size. He claims that: "In nidiculous species (in which the young stay in nest until fledging), the average clutch-size is ultimately determined by the maximum number of young which the parents can successfully raise in the region and at the season in question" (p. 319). Implicitly this idea builds upon two propositions. First, that the selection pressure acting on clutch size is juvenile survival, and secondly, that clutch size is a heritable trait. One can argue that these are Lack's two hypotheses, and that the wellknown paragraph cited above is merely a prediction following from them.

Lack's theory has been revised, for instance by taking into account a possible impact of reproductive effort on adult survival (Williams 1966 and Charnov & Krebs 1974). This refinement connects the traditional clutch size theory with the more general theory of life history strategies (Stearns 1976), and seems plausible theoretically. Positive evidence for this trade-off are accumulating (e.g., Askenmo 1979, Nur 1984, but see Högstedt 1981 and Alerstam & Högstedt 1984).

There is a second important variation on the theme of Lack (1947), which rejects the second of the two propositions, leading to Lack's hypo-

thesis. This recent idea states that clutch size is a trait with great phenotypic plasticity, i.e. that birds are in a sense "able to choose" that number of offspring which is appropriate in a given situation. [This was hinted at by Perrins & Moss (1975), but the idea was developed in more detail by Högstedt (1980) and Drent & Daan (1980).]

There is by now a vast amount of data, and a rich tradition of theory and speculation building upon the work of Lack (1947). In addition to this tradition preserving the first of Lack's two propositions, there are other theories rejecting this; the basis for them are assumptions on parental behaviour and incubation and egg formation ability and so forth (Klomp 1970 and Winckler & Walters 1983).

The unifying concept in the "Lackian tradition" is the emphasis on clutch size dependent juvenile survival in the evolution of reproductive effort and clutch size. Still, most works in the area use juvenile survival as a kind of explanatory tool in the study of clutch size instead of making it an object of study per se. Although the force of mortality on the juveniles is partly under parental control and partly determined by the biotic and abiotic environments (Ricklefs 1969), it is a convention to regard it as something that is beyond the parents capability to control. Clutch size on the other hand, is under much more direct control by the parents and it may therefore change much easier and maybe also faster, be it on an evolutionary or an ecological time scale, than good nest building techniques and other aspects of breeding biology promoting high survival of the young.

The present paper is devoted to the problem how juvenile survival, or reproductive success defined as the ratio, between production of independent young and clutch size, changes in response to adaptive variation (be it genotypic or phenotypic) in clutch size. The basic idea behind the posing of this problem is that this quantity, being a ratio rather than an absolute number, ought to vary within as well as between species in a more predictable and consistent manner than clutch size itself. To give a more precise definition of the problem we can ask: What is the juvenile survival or reproductive success, when clutch size assumes its optimum value?

In a recent paper Alerstam & Högstedt (1983) address this problem and answer that Natural Selection acts in a way making the reproductive success converge towards e^{-1} or roughly 37%. This thesis is indeed provocative, and was soon criticized [Ricklefs (1983) and Stenseth (1984), but see also Alerstam & Högstedt (1983a) and (1984)]. I discuss this and related problems from the background of the analysis of two different

types of models for the joint evolutionary regulation of clutch size and reproductive success. First I focus on a very general type of model in which reproductive success is determined by a large number of different mortality factors, and then I apply this general theory in a model where the mortality factors are acting on two different levels or 'units of mortality'; deaths of single offspring and losses of entire clutches or nests. Finally, I discuss the problem of how interspecific variation in reproductive success might reflect different adaptations for breeding in birds.

DETERMINATION OF REPRODUCTIVE SUCCESS BY MULTIFARIOUS FACTORS

In general the expected outcome of a given pair's reproductive efforts are determined by a manifold of mortality factors acting on the young. This section addresses the problem how individual factors combine into a whole and what characterises the optimum solution when the factors act in concert rather than one at a time. The model presented is basically an extension of earlier models [proposed by, among others, Perrins (1977), Ricklefs (1977) and Lundberg (1985)] to a model allowing for an arbitrary number of clutch size dependent mortality factors, given that these are acting independently of each other in a statistical sense. This is indeed a crucial assumption, because if it fails (and it does so, for instance, when young in larger clutches beg more loudly than do offspring in smaller, thus attracting more predators), we are not allowed to use the rule of multiplication of probabilities, and we should be forced to use conditional probabilities instead. In a sense this assumption also ensures that the whole is the sum of its parts.

Let the proportion of offspring surviving the action of the i^{th} mortality factor be $f_i(x) = e^{-a_i x^{b_i}}$; where $i=1,2,n$, x is the clutch size and a_i and b_i are positive constants (Fig. 1). This function was used by Ricklefs (1977). By the assumption of statistical independence of the factors, the overall reproductive success is given by $\mathcal{S}(x) = f_1(x)f_2(x)\dots f_n(x)$. Hence, the production of independent young from clutches of size x is

$$R_x = x \prod_{i=1}^n e^{-a_i x^{b_i}} \quad (1)$$

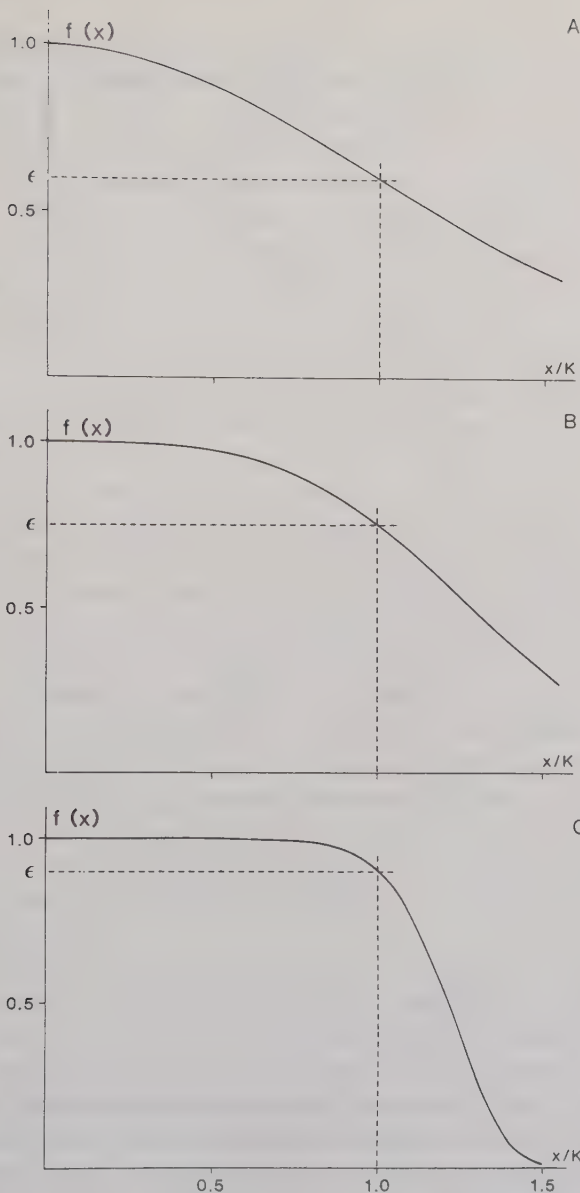


Figure 1. The graphs corresponding to the function $f(x) = e^{-ax^b}$. $a = e^{-1/b}$ and K (see text for formal definitions) describe, respectively, the survival and the optimum clutch that would evolve if the function depicted were the only affecting the survival. Clutch size is given as a fraction of K in the figures, which are drawn for (a) $e^{-1/b} = 0.6$, (b) $e^{-1/b} = 0.75$, and (c) $e^{-1/b} = 0.9$.

By taking the derivative with respect to the clutch size, x , we obtain the optimum clutch size, x^* , as the solution of the equation $1 = \sum_{i=1}^n a_i b_i x^{b_i}$. Now, consider the function $g_i(x) = x e^{-a_i x^{b_i}}$. This represents the production of offspring in a hypothetical state where the i^{th} factor acts in isolation. Under such conditions the clutch size $K_i = (1/a_i b_i)^{1/b_i}$ would evolve, and the resulting reproductive success would be e^{-1/b_i} (c.f., Ricklefs 1977). By observing that $a_i b_i = K_i^{-b_i}$ and substitution into the equation for x^* we then have

$$1 = \sum_{i=1}^n (x^*/K_i)^{b_i} \quad (2)$$

An immediate result from Eq. 2 is that $x^* < K_{\min}$ otherwise the sum does not converge towards unity. The biological interpretation of this is that $K_{\min}$ is the clutch size that would evolve if the limiting factor during the breeding season was the sole factor regulating reproductive success. The combined effect of the n different factors is that the optimum clutch must be less than $K_{\min}$. An argument which is compatible with this principle of limiting factors is that a reduction in clutch size as an evolutionary response to increased predation rate may be optimal because of a compensatory decrease in the number of mortalities owing to starvation assuming that the latter is the limiting factor (e.g., Slagsvold 1982, Lundberg 1985).

The overall reproductive success at optimum $\mathcal{L}(x^*)$ can now be calculated

$$\mathcal{L}(x^*) = \prod_{i=1}^n e^{-a_i x^{*b_i}} = \prod_{i=1}^n \left[\exp - \frac{1}{b_i} \left(\frac{x^{*b_i}}{K_i^{b_i}} \right) \right] \quad (3)$$

or

$$\mathcal{L}(x^*) = \prod_{i=1}^n \left[\exp - \left(\frac{1}{b_i} \right) \right] (x^*/K_i)^{b_i} \quad (4)$$

As the exponents $(x^*/K_i)^{b_i}$ in the product add up to unity, the overall reproductive success at optimum can be regarded as the weighted geometric mean of those survival rates that would have been the result of clutch size evolution occurring in response to each factor taken one at a time. If $b_{\min} = \min_i(b_i)$ and $b_{\max} = \max_i(b_i)$, then

$$e^{-1/b_{\min}} < \mathcal{L}(x^*) < e^{-1/b_{\max}} \quad (5)$$

I shall now discuss three special cases. The first arises when $b_i = b$ for all i . The optimal clutch size becomes a fraction of a kind of mean value of the different K_i -values:

$$x^* = \left[\sum_{i=1}^n (1/K_i)^b \right]^{-1/b} = \text{'mean } K_i \text{'}/n^b \quad (6)$$

The reproductive success is simply $\mathcal{G}(x^*) = e^{-1/b}$. In the case that $b=1$ [which was considered by Alerstam & Högstedt (1983)] this 'mean value' (Eq. 6) degenerates to the harmonic mean value.

The second special case illustrates the importance of the limiting factor in the determination of optimum clutch size. Consider Eq. 2. Choose the lowest real number c such that $b_i \geq c$ for all $i=1, \dots, n$. Substituting all b_i with c we get

$$1 = \sum_{i=1}^n (x^*/K_i)^{b_i} \leq \sum_{i=1}^n (x^*/K_i)^c \quad (7)$$

Now, we have that $K_i < K_{\min}$. By substituting all K_i with $K_{\min}$ we then get

$$1 \leq \sum_{i=1}^n (x^*/K_i)^c < \sum_{i=1}^n (x^*/K_{\min})^c \quad (8)$$

By regarding the last sum in Eq. 9 as a geometric series we get

$$1 < \frac{\left(\frac{x^*}{K_{\min}}\right)^c - \left(\frac{x^*}{K_{\min}}\right)^{c(n+1)}}{1 - \left(\frac{x^*}{K_{\min}}\right)^c} < \frac{(x^*)^c}{(x^*)^c - K_{\min}^c} \quad (9)$$

Therefore, the optimum clutch should always lie in the interval

$$\frac{K_{\min}}{2^{1/c}} < x^* < K_{\min} \quad (10)$$

The biological meaning of this is that the limiting factor is powerful enough to determine limits for the variation of the optimal clutch, independently of the action of the remaining $n-1$ factors.

The third special case is an example demonstrating some of the quantitative properties of the general model. Consider a species in which there are just two clutch size dependent factors. The first factor is defined by $a_1 = -\ln S$ and $b_1 = 1$, that is, $f_1(x) = S^x$. The second factor has the general form $f_2(x) = e^{-ax^b}$. The production of young from clutches that originally contained x eggs is then given by $R_x = x p S^x e^{-ax^b}$, where p is the fraction of the young that escapes clutch size independent mortality,

$S(0 < S \leq 1)$, is what I in the following will label the multiplicative survival rate. This simple model paves the way for the model presented in the following section, and it is also a happy medium model in the recent discussion on the evolutionary regulation of reproductive success (Alerstam & Högstedt 1983, 1983a and Ricklefs 1983). The Alerstam & Högstedt model builds upon the assumption that all mortality factors are multiplicative. The optimum clutch size will be $-1/\ln S$ for birds exposed to such factors when they act in isolation, and the corresponding reproductive success is e^{-1} (Alerstam & Högstedt 1983). In this happy medium model the multiplicative factors act in concert with more general ones and the resulting optimum clutch is obtained by applying Eq. 2 as the solution of the equation

$$1 = -x \ln S + (x^*/K)^b \quad (11)$$

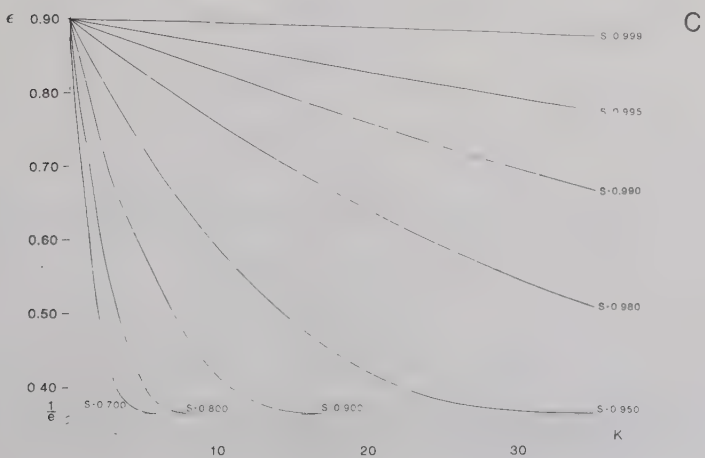
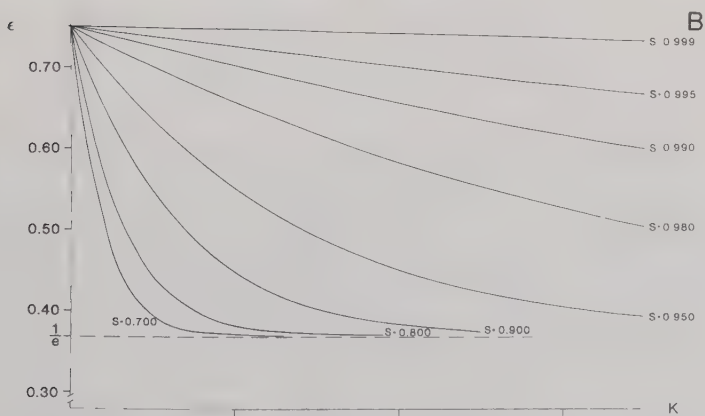
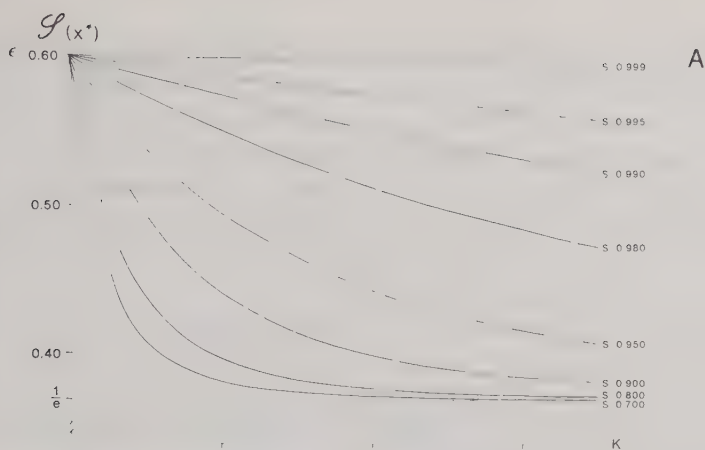
As before we can give an upper for $x^* < \min(-1/\ln S, K)$. The reproductive success is the weighted geometric mean of e^{-1} and $e^{-1/b}$:

$$\mathcal{S}(x^*) = [e^{-1}]^{-x^* \ln S} [e^{-1/b}]^{(x^*/K)^b} \quad (12)$$

I have used Eqs (11) and (12) for calculating the reproductive success $\mathcal{S}(x^*)$ for all conceivable values of S and K for each of three values of $e^{-1/b}$ (Fig. 2). An increase in K leads to a decrease in reproductive success. When K becomes sufficiently large, the reproductive success always converges towards e^{-1} . When K decreases, reproductive success increases and tends towards $e^{-1/b}$ when K is close enough to zero. Hence, by increasing K , i.e. by making the environment more benign as far as the nonmultiplicative factor is concerned, we obviously decreases its relative importance. The reproductive success will approach e^{-1} , as was predicted by Alerstam & Högstedt (1983).

In this context it is worth noting that what Stenseth (1984) actually predicts is that the inclusion of a cost of reproduction in the currency of adult survival leads to an increase in reproductive success to a level which is always higher than e^{-1} .

Figure 2. The reproductive success at optimum $\mathcal{S}(x^*)$ as a function of S , the multiplicative survival rate, and the most productive brood size K for the within clutch component. The values of $\epsilon = e^{-1/b}$ are those given in Fig. 1.



DETERMINATION OF REPRODUCTIVE SUCCESS BY FACTORS ACTING WITHIN AND BETWEEN CLUTCHES

In this section we consider reproductive success not as a product of many different, statistically independent factors, but as a result of processes acting on different levels. That is we assume that there are two units of mortality; individual offspring and entire clutches. All conceivable factors should then ideally be possible to assign to either unit, e.g., starvation is factor acting predominantly within clutches, whereas predators, bad weather are factors acting mostly on the entire clutch level. This dichotomy of factors affecting the survival of avian offspring has been stressed earlier by (for example) Ricklefs (1969), Perrins (1977) and Lundberg (1985).

Consider a species laying x eggs. A given pair can have, at any stage of the nesting season any number i of offspring ($i = 0, 1, \dots, x$), i.e., a clutch can be in any of $x+1$ states. The mortality factors cause transitions between these states, such that the factors acting on the clutch level leads to transitions of the type $i \rightarrow 0$, and those at the individual level to transitions of the type $i \rightarrow i-1$ (Fig. 3). I will use an extension of a continuous time Markov chain called the pure death process (Pielou 1977) for deriving a probability density function describing the probabilities for the $x+1$ possible outcomes of breeding.

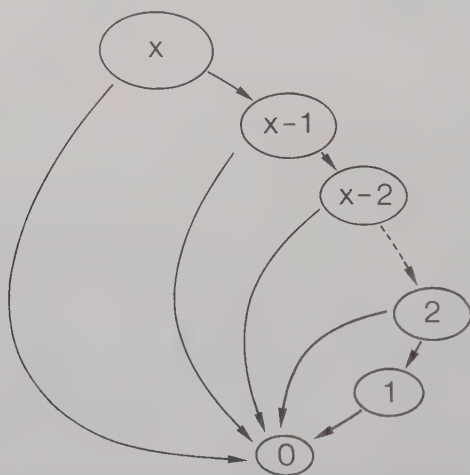


Figure 3. Graph describing the $x+1$ possible states for a clutch that initially contained x eggs. Transitions between states are of two kinds $i \rightarrow i-1$ and $i \rightarrow 0$ and indicated by arrows in the graph.

Let the probability that a clutch is in state i at a given time t from the onset of breeding be $P_i(t)$. Further, let the instantaneous death rate of young within clutches be μ and the death rate of entire clutches be m . The probability for transitions of the type $i \rightarrow i-1$ is then μ . (Pielou 1977) whereas the probability for transitions of the type $i \rightarrow 0$ is m . The changes in the probabilities $P_i(t)$ overtime can be described by the following system of linear differential equations:

$$\frac{dP_x(t)}{dt} = - (x\mu + m)P_x(t), \quad (13)$$

$$\frac{dP_i(t)}{dt} = \mu(i+1)P_{i+1}(t) - (i\mu + m)P_i(t), \quad 1 \leq i < x, \text{ and}$$

$$\frac{dP_0(t)}{dt} = \mu P_1(t) + \sum_{i=1}^n mP_i(t) = \mu P_1(t) + m(1-P_0(t)).$$

This formulation assumes that all eggs are laid simultaneously at time $t=0$. However, this poses no problem unless partial losses are very common during laying. More severe is that m and μ are not allowed to change over time, an inclusion that would make the model much less tractable. The system is solved in a similar way as the pure death process (see Pielou 1977). We calculate the probability density function for time T (the age at independence) given the boundary condition that all nests contain x eggs to begin with (i.e., let $P_x(0) = 1$ and $P_i(0) = 0, 0 \leq i < x$). The probability for producing exact R independent young is given by

$$P_R = \binom{x}{R} e^{-mT} e^{-\mu TR} (1 - e^{-\mu T})^{x-R}, \quad R > 0, \text{ and} \quad (13a)$$

$$P_0 = 1 - e^{-mT} + e^{-mT} (1 - e^{-\mu T})^x \quad (13b)$$

The mean production of young $\bar{R}$ and the variance σ_R^2 around the mean are

$$\bar{R} = x e^{-mT} e^{-\mu T}, \quad \text{and} \quad (14a)$$

$$\sigma_R^2 = x e^{-mT} e^{-\mu T} [(1 - e^{-\mu T}) + x e^{-\mu T} (1 - e^{-mT})] \quad (14b)$$

respectively. Technically we have two kinds of processes acting simultaneously; by setting $m=0$ we get the traditional pure death process back, and hence the production will be a binomial random variable, whereas if $\mu=0$, R becomes a kind of Bernoulli random variable [with two possible outcomes, 0 and x (c.f., Ross 1972)], We can arrive at Eqs. (13a-b) in a much more heuristic manner: If the deaths within clutches occur independently random with the probability $1-e^{-\mu T}$ it is reasonable to assume that the number of survivors are distributed binomially, but since just a fraction e^{-mT} of the clutches survive we have to multiply the binomial distribution formula with this factor [we then get Eq. (13a)] Zero production can arise in two mutually exclusive ways, first, the clutch may not escape the between clutch mortality factors (this occurs with probability $1-e^{-mT}$) and, secondly, it may do so but all chicks may die anyway because of within clutch factors. The probability that they all die is $(1-e^{-\mu T})^x$ but this has to be multiplied with the factor e^{-mT} as they did escape the between clutch factors. Adding the probabilities for the two cases we get Eq. (13b).

Biologically, the model says just little more than that the chicks has a type II survivorship curve up to independence (indeed, this is an assumption). For the theory to be useful we must add assumptions about the clutch size dependence of the parameters m , μ and T . There is no obvious way to do this, and I will make it in a way that might not be generally valid. Let $mT = -x \ln S$ and $\mu T = ax^b$. Thence, it follows by substitution into Eq. (14a) that

$$\bar{R} = xS^x e^{-ax^b} \quad (15)$$

This model is thus identical with the third special case treated in the preceding section, in that they have the same optimum clutch size. In the next section I will return to the properties of the optimum.

Another possible way of introducing clutch size dependence is to make the parameters linear functions of x . The function for T will then have a slope of at least unity, as many birds lay one egg a day. The slope may exceed unity if the rate of development is retarded by the addition of young. This seems to be true for great tit in southern Sweden (Smith, pers. comm.) whereas brood size manipulation does not affect the rate of development for pied flycatcher (Högstedt, pers. comm.). The intercept of the T -function will equal the length of the incubation period plus the minimum time span from hatching to independence. m and μ may also increase

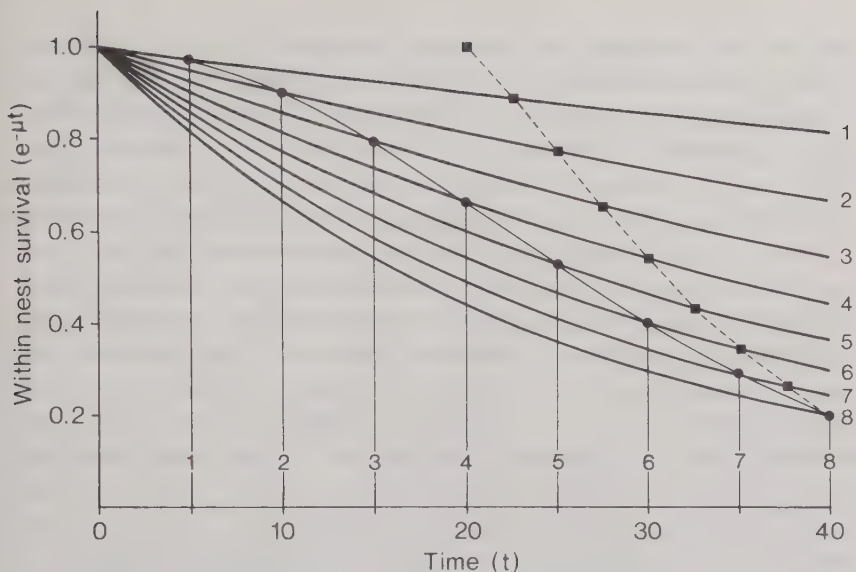


Figure 4. An illustration of how clutch size dependence can be introduced by letting the instantaneous death rate μ and the age at independence T be linear functions of the clutch size. The curve family describes the decline in the fraction of survivors within nests over time for different clutch sizes. The vertical lines represents different ages at independence (T) for different clutch sizes. The graph through the intersections between those lines and curves corresponding to the same clutch sizes is the function e^{-ax} . The dashed curve is derived in a similar way, but shows the case when there is a minimum age at independence.

with clutch, but with slopes and intercepts of which we do nothing. I assume that the intercepts are zero, giving survival rates of unity when clutch size is zero. Now, by letting m be independent of clutch size, but letting both μ and T increase linearly as outlined above, but making the simplification that the intercept of the T -function equals zero, we get Eq. (15). b will in this case equal 2. I neglect the T -function's intercept in order to avoid a first degree term in the product μT . These arguments are illustrated graphically in Fig. 4.

I shall briefly mention that by relaxing the restricting assumptions made in the pure death process one also affects the values of a and b . In the discussion of these parameters we assumed that the instantaneous death rate of chicks, μ , was a linear function of the initial clutch size, independent of which state the clutch was in. That is, the occurrence of some deaths does not influence the fate of the remaining offspring. I have

made numerical investigations of a model in which μ varies both with initial clutch size and with state (Lundberg, unpubl.). The latter type of variation was introduced such that the likelihood of further deaths either increased or decreased with the number of deaths that had already occurred in the clutch. This leads to either an acceleration of the death process (e.g., owing to the spread of an infection) or a retardation (e.g., owing to a decreased level of within clutch competition). The consequences for the parameters of this complication is that an acceleration of the death process leads to substantial increase in a , whereas a retardation causes a decrease. The impact on b is generally smaller, and in the opposite directions.

The constancy of m seems plausible to me because the instantaneous death rate of clutches depend on factors that might be correlated over relatively large areas, e.g., predator density, climate, nest type and so on, whereas exponents to the factors 'in terms of length of time, no. of nest visits, food begging calls, incidents of unsufficient parental supervision, etc' [Alerstam & Högstedt 1983 (p. 140)] in a wide sense is easily translated into a clutch size dependence.

The validity of these considerations concerning the parameters a and b does not change the basic properties of the model. However, there seems to be a qualitative difference between them, in that the former is highly influenced by environmental factors, whereas b is uniquely determined by how the clutch size dependence is introduced. That is, it is a basic property of a species breeding biology.

WITHIN SPECIES VARIATION IN REPRODUCTIVE SUCCESS

Clutch size as well as reproductive success varies a great deal within species. Large scale geographic variations have been interpreted as adaptive (Lack 1947) and so have local ones between for example feeding territories (Högstedt 1981). Both types of variation can be discussed from the point of view of the model proposed in the present paper, given that the cause of the variation is differences in the clutch size dependence of the survival of the young. The main task of this section is to meld the two models proposed, so that we can not only predict optimum clutch size and the corresponding reproductive success, but also the distribution of reproductive outcomes arising from a single clutch size as outlined in previous section. The presentation is made such that it mimics various kinds of data often available in field studies.

Before doing this I will make a digression in the problem how the parameters of the model can be estimated from data. In the following I will discuss two kinds of field studies. By a 'survey' I understand a study in which clutch size and reproductive outcome is recorded for a large number of clutches, whereas an 'experiment' means the collection of the same kind of data for natural as well as manipulated clutch sizes (i.d., experimentally increased or decreased ones).

It is obvious that the interpretation of a field study, be it a survey or an experiment, depends very much on whether or not total nest failures are included in the data set, and whether a classification of mortality factors with respect to their level of action is possible at all. Thus, imagine a field study of the production of young from clutches of a certain size, in which total failures are excluded. The mean production observed is then given by $E(R|R>0) = \sum P_i / (1 - P_0)$ or

$$E(R|R>0) = x e^{-ax^b} / [1 - (1 - e^{-ax^b})^x] = x e^{-ax^b}, \quad (16)$$

where the within clutch mortality is assumed to be non-multiplicative ($\mu T = ax^b$). The quantity $(1 - e^{-ax^b})^x$ is the fraction of clutches that have zero production owing to within clutch mortality factors. When this contribution is low, the second approximate equality is valid. Given this approximation, b , S and K can be easily estimated. K is the most productive brood found in a brood size manipulation experiment including clutches that originally had the same size, but excluding only total failures. b is calculated from the survival of these clutches, which is $e^{-1/b}$. Finally, S is calculated from the slope in a regression of $\log(1 - P_0)$ vs. experimental clutch size.

If the approximation in Eq. 16 fails, we can use the truncated version of Eq. 13.

$$P(R|R>0) = \binom{x}{R} \frac{e^{-ax^b R} (1 - e^{-ax^b})^{x-R}}{1 - (1 - e^{-ax^b})^x} \quad (17)$$

Assume that we have data on reproductive output from n clutches $R_1, R_2, \dots, R_n$ and that the original clutch size was x for all of them. Let $q = e^{-ax}$. Then a maximum likelihood estimate of q is given by the solution of the equation

$$\sum_{i=1}^n R_i / nx = q / (1 - (1-q)^x). \quad (18)$$

This equation must as a rule be solved numerically.

In the following discussion I assume that Högstedt's (1981) finding that birds may have an adaptive phenotypic variation in clutch size is applicable. A territory can be in either of two conditions. If $K < 1/\ln S$, then the within clutch factor is the limiting. Clutch size is K-limited. If the inequality goes in the opposite direction, clutch size is limited by the between clutch factor or S-limited.

Assuming that the birds in an area are predominantly K-limited we may find that the most productive brood size estimated experimentally as outlined above by excluding total failures, exceeds their natural clutch size. Then a clutch size reduction has occurred, because of the effect of the between clutch factor is to decrease the optimum somewhat below K . This phenomenon was labelled clutch size reduction by Lundberg (1985).

A variation in clutch size is caused by a variation in S or K or both between territories. I will give qualitative predictions of the behaviour of reproductive success, total failures and the distribution of reproductive outcomes under three conditions. First, I will predict the behaviour of these quantities in relation to manipulated clutch size (experiments as defined above). Secondly, I will do this in relation to natural clutch size, that is, I predict the outcomes of surveys. The variation in clutch size is thought to arise owing to variation in either K or S (by varying one parameter while keeping the other constant).

Reproduction success - (i) When clutch size is reduced, reproductive success increases, whereas it decreases in expanded clutches (Fig. 5a). A non-linearity of a plot of $\log S$ versus experimental clutch size indicates that a significant fraction of the deaths are due to non-multiplicative within clutch factors. (ii) When it is only K that determines the differences in quality between breeding areas, the reproductive success will not be, or will be just, slightly negatively correlated with optimum clutch size, (iii) whereas there will be a strong positive correlation when the differences are due to a change in S .

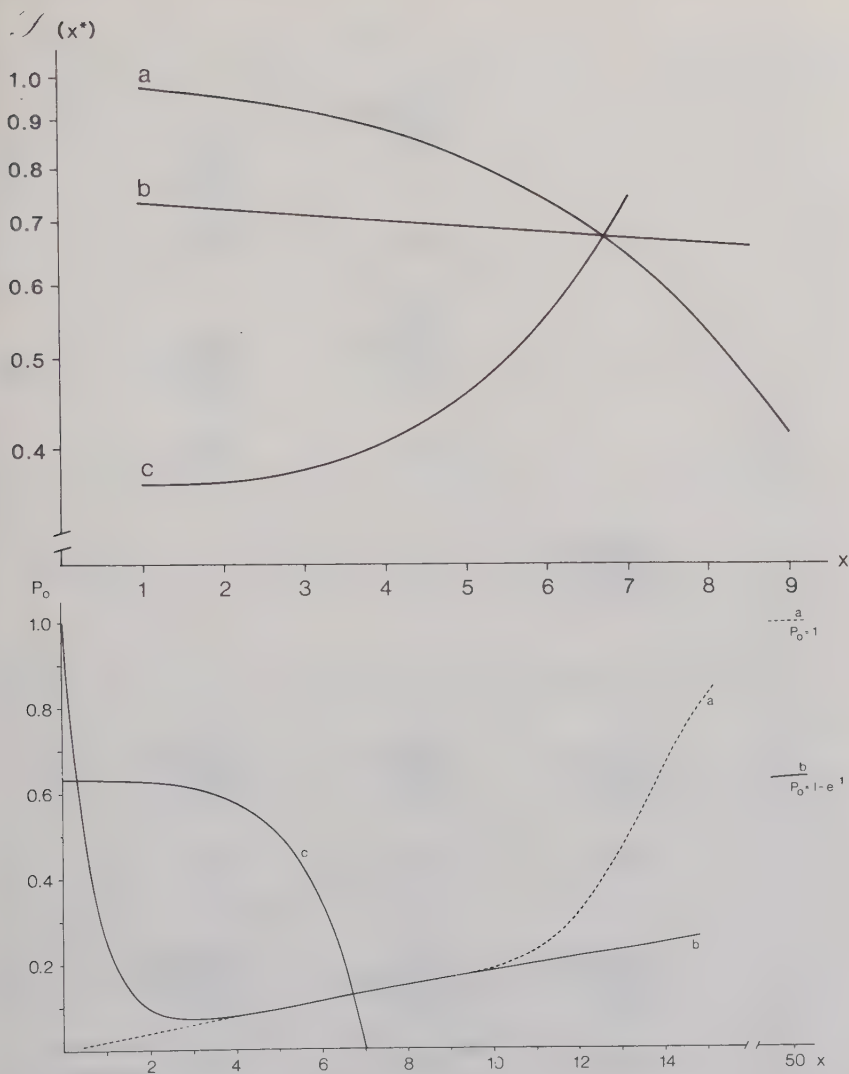


Figure 5. (A) The reproductive success $\mathcal{S}(x^*)$ as a function of clutch size. Graph a is the hypothetical outcome of a brood size manipulation experiment of the kind performed by Högestedt (1980). The abscissa corresponds to manipulated brood (or ideally clutch) size. The parameters are $K=7$, $e^{-1/b}=0.75$ and $S=0.98$, corresponding to an optimum clutch $x^*=6.7$. Graph b represents the reproductive success for unmanipulated clutches when K is the parameter causing the variation in clutch size. Except for K the parameters are the same as for graph a. Graph c depicts the same kind of data as b but with S as the varying parameter. Except for S , the parameters are the same as graph a.

(B) Variation in P_0 as a function of clutch size, for the same three cases as in (A). Graph a shows P_0 for manipulated broods, b the variation in P_0 in natural clutches when K varies, and c when S varies. The parameters are in all cases as in Fig. 5a.

Complete failures - (i) When brood size is manipulated experimentally, P_0 will increase almost linearly up to the naturally occurring optimal clutch size but will then approach unity relatively fast (Fig. 5b). This dramatic increase in total losses is mostly due to the within clutch mortality factors. (ii) When K determines the differences in quality between breeding areas there is a slight increase in P_0 with optimum clutch size. However, below a certain clutch there will be a negative correlation, showing that a poor environment, leading to high within clutch mortality contributes to the total nest failures. (iii) When S determines the differences between breeding areas, P_0 will decrease with optimum clutch size, slowly to begin with, but very fast when the clutch size approaches K.

Around optimum clutch size the P_0 values we would get in response to a brood size experiment will follow those we would get to natural clutches. At greater distance from optimum the experimental curve will deviate. This similarity arises only in species where the differences in optimum clutch size are due to differences in K, and S is held constant.

The distribution of reproductive outcomes - (i) The mode of the distribution will for experimentally expanded broods lie approximately at their natural optimum (Fig. 6), giving a larger variance in R than for natural clutches of comparable size. In experimentally reduced clutches the distribution will be skewed towards the larger reproductive outputs, reflecting the high survival of these clutches. (ii) When a variation in K is the causal factor behind the variation in clutch size, the shape of the distribution will be roughly the same for all clutch sizes. (iii) For low values of S, under S-limitation, the distribution will be very u-shaped, but this tendency will disappear when S increases and we reach the breakeingpoint when the birds are K-limited.

There is an interesting similarity between experimentally reduced clutches and natural ones in areas with low survival of entire clutches but high of individual offspring. In the latter the distribution of reproductive outputs is heavily bimodal, such that clutches with nonzero production have a relatively high survival, and the truncated distributions of the two cases are almost identical. In a sense it is the balance between S and K that gives the shape of the distribution; if K is increased beyond what is shown in these examples we will again get S-limitation the same type of u-shaped distribution showing that the between clutch factors are limiting.

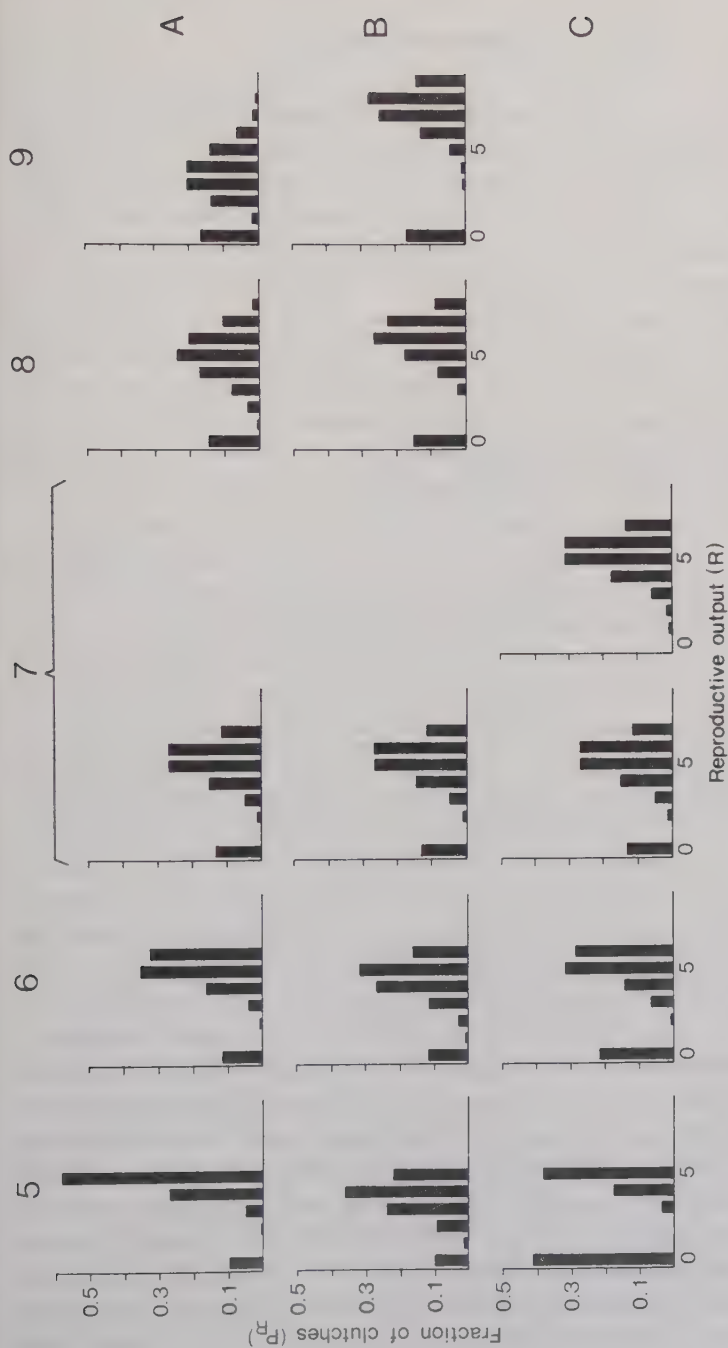


Figure 6. The distribution of reproductive output for the three cases depicted in Fig. 5 (rows) for clutch sizes 5 through 9 (columns). A, B and C represents, respectively, a brood size manipulation experiment, differences in the distribution of reproductive output (R) due to variation in K and due to variation in S . The right-most distribution in row C shows the case $S = 1$. In the other cases, the parameters correspond approximately to those used in Fig. 5a.

BETWEEN SPECIES VARIATION IN REPRODUCTIVE SUCCESS

Alerstam & Högstedt (1983) summarises data on reproductive success of a number of species with parental care, including birds, mammals and prehistoric as well as modern man. They are able to demonstrate a distribution heavily skewed towards e^{-1} , especially among nidifugous birds. However, there are some deviations, and for the avian examples they are mostly pronounced among the nidiculous birds.

Alerstam & Högstedt (1983) discuss these exceptions in some detail, giving separate explanations for those deviating most. They discuss this from the point of view that these creatures might not have been able to realize their optimum clutch for various reasons. They also note the possibility that the reproductive success in many cases might be overestimated (for example for hole nesting birds living in nest boxes). I grant that both lines of argument might be correct, but the fact that there is a significant negative correlation between the reproductive success and clutch size for the data given by Alerstam & Högstedt (1983)(Fig. 7), particularly strong for the nidiculous birds, indicates that there is no need for special explanations for each deviating species. Instead, these patterns call for a general explanation. In this section I will make an admittedly speculative attempt to explain the pattern that emerges in Fig. 7.

Recall Eq. 12, the meaning of which is that reproductive success for a given species is the geometric mean of two factors, which may act on different levels. As shown in Fig. 2, an increase in K will lead to a decrease in $\mathcal{L}_i(x^*)$ from $e^{-1/b}$ to e^{-1} . This is accompanied by an increase in x^* . Within species such a change in K will be hardly detectable (see the preceding section). However, if we superimpose a decrease in S the effect is pronounced, and may explain the negative correlations in Fig. 7.

To account for the differences between nidiculous and nidifugous species we have to qualify this very general statement by making the distinction between the two levels of mortality. Nidifugous species are expected to have a relatively low reproductive success, around 37 % for the following reasons: First, deaths owing to clutch size dependent factors seem to act on just one level at a time; during laying and incubation we have losses on the nest level that are necessarily clutch size dependent as it takes longer time to lay a larger clutch than a smaller one. During this period we have some deaths on the individual level, but they seem to be due to clutch size independent factors as egg infertility [which, howe-

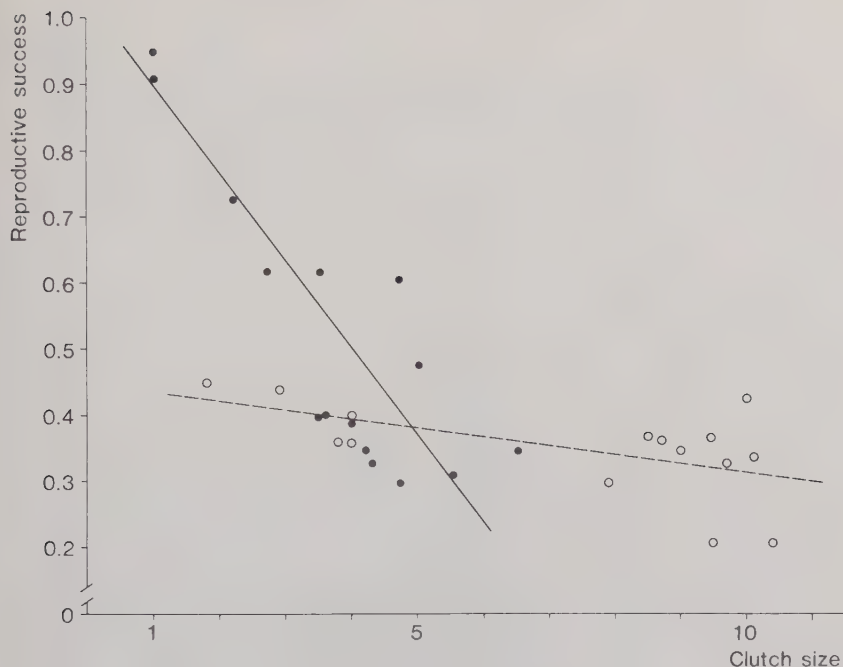


Figure 7. Reproductive success as a function of clutch size for nidicolous (filled dots) and nidifugous (rings) bird species. For both kinds, there is a significant negative correlation ($r_s = -0.73$, $P < 0.01$ and $r = 0.57$, $P < 0.05$, respectively. $n = 15$ in both cases). Data from Alerstam & Högstedt (1983).

ver, may be weakly correlated with clutch size (Lundberg 1985)]. After hatching the chicks soon leave the nest, and after that each of them becomes an independent (in a statistical sense) unit of mortality. Secondly, after leaving the nest predation often becomes the most important cause of clutch size dependent deaths. The parents' ability to protect their young depends on clutch size (Safriel 1975). If food shortage is a rare event then the rate of development should be clutch size independent. This means that we can expect that the Alerstam & Högstedt (1983) model should be applicable for nidifugous species, and it is indeed corroborated by their data.

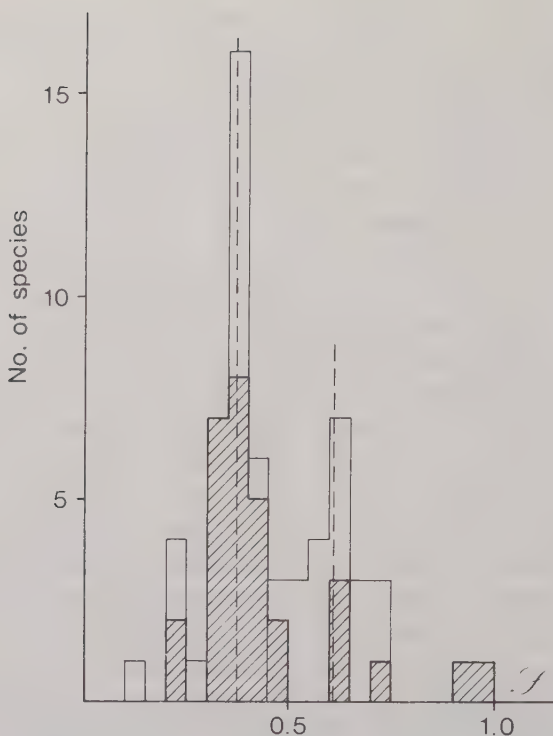


Figure 8. The distribution of reproductive success for 59 bird species. The dashed lines represents the hypothetical reproductive success-values e^{-1} and $e^{-1/2}$ discussed in text. The dataset is collected from Clark & Wilson (1981) and Alerstam & Högstedt (1983). The hatched histogram is based on data from the latter source, whereas the open represents the total dataset. Alerstam's & Högstedt's data are more appropriate for the testing of the ideas in the present paper as clutch size independent losses during incubation are excluded, and losses between fledging and independence are included.

In contrast, in nidiculous species, the young are totally dependent on their parents food provisioning and the considerations leading to the conclusion that the parameter b might equal 2 seem to be applicable. Ideally, if there is no between clutch mortality the reproductive success would be $e^{-1/2}$ or roughly 61 %. This might be the situation for hole nesting birds. Fig. 8 depicts the distribution of reproductive successes of 59 bird species. This distribution, does in fact have two peaks, one around 37 % and another around 61 %, containing 16 and 7 species, respectively.

REFERENCES

- Alerstam, T. & Högstedt, G. 1983. Regulation of reproductive success towards e^{-1} (= 37 %) in animals with parental care. - *Oikos* 40: 140-145.
- Alerstam, T. & Högstedt, G. 1983a. Optimal reproductive success - reply to Ricklefs. - *Oikos* 41: 286-288.
- Alerstam, T. & Högstedt, G. 1984. How important is clutch size-dependent mortality? - *Oikos* 43: 253-254.
- Askenmo, C. 1979. Reproductive effort and return rate of male pied flycatchers. - *Am. Nat.* 113: 748-752.
- Charnov, E.I. & Krebs, J.R. 1974. On clutch size and fitness. - *Ibis* 116: 217-219.
- Clark, A.B. & Wilson, D.S. 1981. Avian breeding adaptations: Hatching asynchrony, brood reduction and nest failure. - *Quart. Rev. Biol.* 56: 253-277.
- Drent, R.H. & Daan, S. 1980. The prudent parent: Energetic adjustment in avian breeding. - *Ardea* 68: 225-252.
- Högstedt, G. 1980. Evolution of clutch size in birds: Adaptive variation in relation to territory quality. - *Science* 210: 1148-1150.
- Högstedt, G. 1981. Should there be a positive or negative correlation between survival of adults in a bird population and their clutch size? - *Am. Nat.* 118: 568-571.
- Klomp, H. 1970. The determination of clutch-size in birds, a review. - *Ardea* 58: 1-120.
- Lack, D. 1947. The significance of clutch-size. - *Ibis* 89: 302-352.
- Lundberg, S. 1985. The importance of egg hatchability and predation in clutch evolution in altricial birds. - *Oikos* 45: 110-117.
- Nur, N. 1984. The consequences of brood size for breeding in blue tit I. Adult survival, weight change and the cost of reproduction. - *J. Anim. Ecol.* 53: 479-496.
- Perrins, C.M. 1977. The role of predation in the evolution of clutch size. In: Stonehouse, B. & Perrins, C.M. Eds, *Evolutionary Ecology*. - Macmillan Press, London.
- Perrins, C.M. & Moss, D. 1975. Reproductive rates in the great tit. - *J. Anim. Ecol.* 44: 695-706.
- Pielou, E.C. 1977. *Mathematical ecology* - John Wiley & Sons, New York.
- Ricklefs, R.E. 1969. An analysis of nesting mortality in birds. - *Smithsonian contrib. Zool.* 9.
- Ricklefs, R.E. 1977. A note on the evolution of clutch size in altricial birds. In: Stonehouse, B. & Perrins, C.M., Macmillan Press.
- Ricklefs, R.E. 1983. A comment on the regulation of reproductive success towards e^{-1} . *Oikos* 41: 284-285.
- Ross, S.M. 1972. *Introduction to probability models*. - Academic Press, New York.
- Safriel, U.N. 1975. On the significance of clutch size in nidifugous birds. - *Ecology* 56: 703-708.
- Stearns, S.C. 1976. Life history tactics: A review of the ideas. - *Quart. Rev. Biol.* 51: 3-47.
- Slagsvold, T. Clutch size variation in passerine birds: The nest predation hypothesis. - *Oecologia* 54: 159-169.
- Stenseth, N.C. 1984. Optimal reproductive success in animals with parental care. - *Oikos* 43: 159-253.
- Winckler, D.W. & Walters, J.R. 1983. The determination of clutch size in precocial birds. In: Johnston, R.F. ed. - *Current Ornithology* 1. - Plenum, New York.
- Williams, G.C. 1966. Natural selection, the costs of reproduction and a refinement of Lack's principle. - *Am. Nat.* 100: 687-690.

BIRD MIGRATION PATTERNS:
CONDITIONS FOR STABLE GEOGRAPHICAL POPULATION SEGREGATION

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ABSTRACT

Migration costs, increasing with increasing distance, and asymmetric competition between stationary and migratory individuals, and between individuals arriving early and late to breeding and winter sites, lead to latitudinal as well as longitudinal segregation between migratory bird populations. A chain migration pattern (winter quarters of different populations are situated in the same latitudinal sequence as breeding areas) evolves when there are migration costs but no asymmetric competition, or with asymmetric competition either for breeding or wintering resources. In contrast, asymmetric competition in both breeding and winter quarters is a necessary but not sufficient condition for the evolution of leapfrog migration (winter and breeding areas in a reversed latitudinal sequence).

INTRODUCTION

The breeding and wintering ranges of many migratory bird species have a wide latitudinal extension. Nilsson (1858) proposed that the winter quarters of different populations are situated in the same latitudinal sequence as their breeding areas, a pattern we will call "chain migration". Palmén (1874) compiled information about the nonbreeding occurrence of several species breeding in the North Palaearctic. On this basis, he concluded that, besides chain migration, a "leapfrog migration" pattern is often manifest, both within species and between closely related and ecologically similar species. According to this pattern the latitudinal sequence of different populations' wintering areas is the reverse of their breeding areas, i.e. the most northerly breeding populations winter farthest to the south, overflying southerly breeding populations.

Ringing results have since confirmed Palmén's conclusion, and Salomonsen (1955) reviewed many examples of chain and leapfrog migration, as well as cases with no wintering segregation between different breeding populations. In some species the situation is complex, with elements of both chain and leapfrog migration. Salomonsen noted that a leapfrog tendency is widespread, whereas chain migration "is not so commonly established as should be expected".

Salomonsen (1955) stressed the importance of intraspecific competition as an ultimate selection force for the development of wintering segregation between populations, but he made no attempt to determine which conditions lead to the different migration patterns observed.

Alerstam & Högstedt (1980) suggested that leapfrog migration primarily arises because of a differential advantage of wintering close to the bree-

ding sites, between southerly (temperate) -breeding and northerly (arctic) -breeding populations. In the former populations, birds remaining during winter in the temperate climatic zone can migrate to their adjacent breeding areas as soon as suitable spring conditions develop. Such an early spring arrival, adapted to yearly variations in spring climate, may constitute an important advantage in the competition for breeding resources. This is not feasible for birds breeding in the arctic zone, which they must leave during winter, thereby losing the possibility of adjusting spring migration to the yearly variation in spring development within their breeding range. Hence, arctic birds may migrate far to the south, avoiding competition with temperate populations, relying on their circannual clock to return to their breeding range at the optimal average time.

This idea was criticized by Pienkowski, Evans & Townshend (1985), suggesting an alternative hypothesis: They assumed that, because of migration costs, it is advantageous for birds to winter as close to their breeding grounds as possible. Dominant individuals, from populations with a relatively large average body size, will outcompete individuals from populations with a smaller body size, forcing the latter birds to continue their autumn migration to more southerly latitudes. Hence, leapfrog migration will occur when southerly-breeding populations, for reasons unknown, have the largest average body size, while the reverse will lead to chain migration.

Alerstam & Högstedt (1985) pointed out that there exist evidences contrary to both of these hypotheses. They also noted that a more general understanding of the conditions promoting geographical wintering segregation between different breeding populations, and breeding segregation between different wintering populations, is still lacking.

Asymmetric competition between stationary and migratory individuals, and between individuals arriving early and late, probably is of crucial importance in the evolution of bird migration (von Haartman 1968, Alerstam & Enckell 1979). Northerly residents (throughout this paper we adopt a northern hemisphere-perspective) have temporal priority to the most favourable nest-sites and breeding territories. Migration to southerly wintering areas will evolve when the associated benefit in survival more than compensates for the disadvantage in the competition for breeding resources (von Haartman 1968).

Analogously, southerly residents have priority to the most favourable wintering sites. Migration to northerly breeding areas will evolve when the benefit in reproduction more than compensates for the competitive

disadvantage in the southerly survival areas. Consequently, the evolution of bird migration will be facilitated in situations with a not too strong influence of asymmetric competition associated with temporal priority, like in highly seasonal and unpredictable habitats, or with resources that are difficult to monopolize and defend (Alerstam & Enckell 1979). But this does not preclude that there may be many instances where asymmetric competition associated with temporal priority to breeding or wintering sites, or both, is in operation between individuals from different migratory (and resident) populations.

We will investigate the importance of such asymmetric competition, under different regimes of migratory costs and resource availability for breeding and survival, for the development of bird migration patterns. We will try to throw light, besides on latitudinal patterns, also on longitudinal segregation between migratory populations, i.e. "parallel migration" in Salomonsen's (1955) classification, including the development of migratory divides.

LATITUDINAL SEGREGATION

(A) A population simulation model.

Let a matrix $X = (x_{ij})$ describe the migration pattern of a species. Each entry x_{ij} of this matrix denotes the number of individuals breeding at site i and wintering at site j . Sites are numbered latitudinally from north to south, and $i \leq j$. For our calculations we have adopted a system with 5 latitudinal sites. Basic types of migration patterns are exemplified in Fig. 1.

The change in population x_{ij} from one year (breeding population size) to the next is given by:

$$(x_{ij})_{t+1} = (x_{ij})_t R_{ij} P_{ij} S_{ij} Q_{ij} \quad (1)$$

where R_{ij} is the reproductive rate, S_{ij} the winter survival, and P_{ij} and Q_{ij} the autumn and spring migration survival, for individuals breeding at site i and wintering at site j .

The reproductive rate is given by:

$$R_{ij} = B_i \left(1 - K_{b,i}^{-1} \sum_k (\alpha_{i,jk} x_{ik}) \right) \quad (2)$$

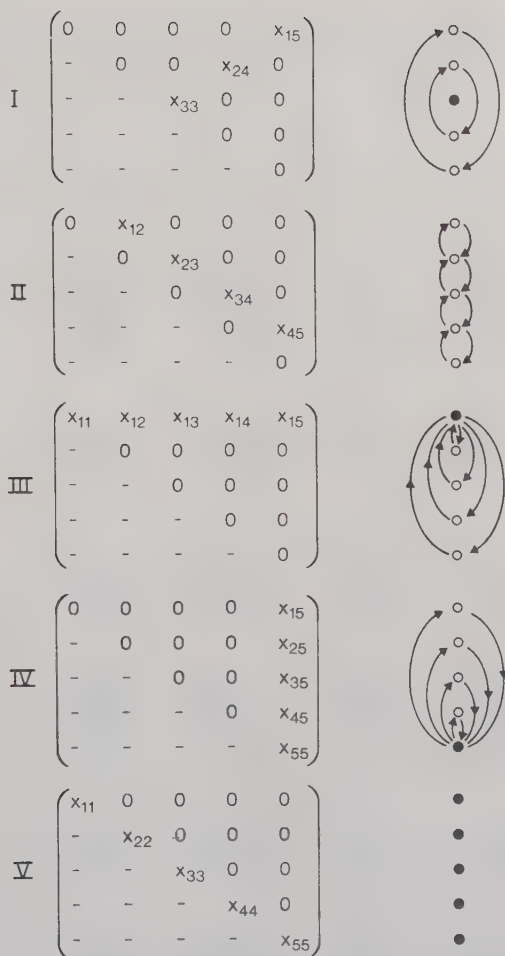


Figure 1. Matrices showing some basic types of latitudinal bird migration patterns. Rows correspond to different breeding latitudes and columns to wintering latitudes. Migrations between the five latitudinal sites are illustrated for each matrix to the right. Filled symbols denote sites with a resident population. Type I (characterized by a left-sloping matrix) corresponds to leapfrog migration and type II (right-sloping matrix) to chain migration. Non-sloping, horizontal (type III) or vertical (IV) matrices, or a combination of both, represent instances without latitudinal breeding or wintering segregation, or both. Type V denotes a resident species.

where B_i is the breeding suitability at site i (i.e. the reproductive output without competition), $K_{b,i}$ is a measure of the total availability of breeding resources at this site, and $\alpha_{i,jk} = \exp[a(j-k)]$ is the competition effect at breeding site i of individuals from population x_{ik} on x_{ij} . Hence, with $a > 0$ asymmetric competition takes place, favouring individuals from northerly wintering sites because they presumably can arrive first to the breeding site. With $a = 0$, individuals from all different wintering sites compete on equal terms.

Migration costs are assumed to be proportional to migration distance, such that $p_{ij} = S_1 - d_1(j - i)$, and $q_{ij} = S_2 - d_2(j - i)$ for $0 < p, q, S_1, S_2 \leq 1$.

The winter survival is given by:

$$S_{ij} = W_j \left(1 - K_{s,j}^{-1} \sum_v (\beta_{iv,j} x_{vj} R_{vj} p_{vj}) \right) \quad (3)$$

where W_j is the wintering suitability at site j (i.e. the winter survival without competition, $0 \leq W_j \leq 1$), $K_{s,j}$ is a measure of the total availability of winter survival resources at site j , and $\beta_{iv,j} = \exp[c(v - i)]$ is the competition effect at wintering site j of individuals from population x_{vj} on x_{ij} . With $c > 0$ asymmetric competition is assumed, favouring individuals from southerly breeding areas because they presumably can arrive first to the wintering site. With $c = 0$, winter competition takes place on equal terms between all individuals.

Computations for a particular set of conditions (defined by the variables in equations 1-3), were initiated with all entries x_{ij} in the migration pattern matrix equal, and lasted 150 iterations (breeding and wintering cycles). After that number of iterations the resulting migratory pattern generally was stable or almost stable (differing to an insignificant extent from the stable pattern emerging after additional iterations). Supplementary computations indicated that the emergent stable migration patterns were not dependent on the set of initial x_{ij} values.

We will concentrate our analysis to the situation where breeding is only possible at sites 1, 2 and 3, and wintering only at sites 3, 4 and 5. Results demonstrating the effect of asymmetric competition and migration costs are presented in Figs 2 and 3, respectively. When assuming latitudinal gradients in breeding and wintering suitability, we have restricted our attention to what is probably the most general and realistic conditions, i.e. a breeding suitability increasing towards the north and a wintering suitability increasing towards the south.

Latitudinal gradients
in breeding (B) and wintering (W) suitability

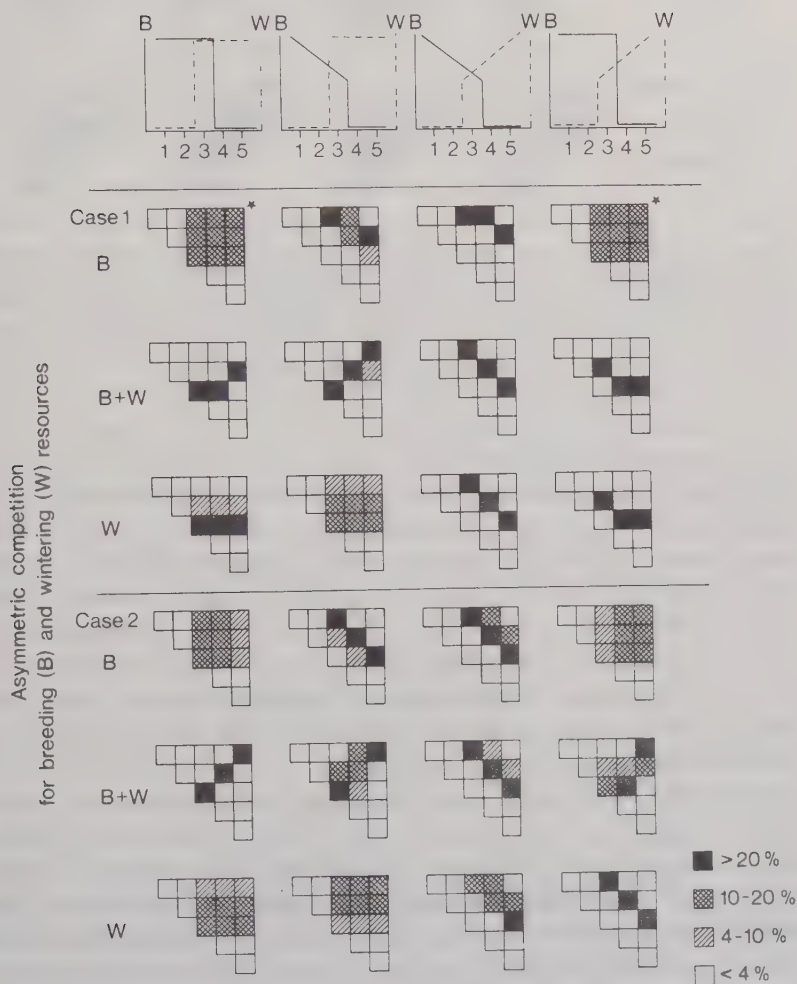


Figure 2. Stable migration patterns under different latitudinal gradients in breeding and wintering suitability (four conditions, one for each column, as illustrated), and with asymmetric competition either for breeding ($a > 0$) or wintering ($c > 0$) resources or both ($a, c > 0$). In case 1 the ratio K_1/K_2 is unity, while in case 2 there are relatively more resources for winter survival, $K_1/K_2 = 3$. Migration costs have been excluded in all instances ($d_1^s, d_2^s = 0$). Matrices show relative sizes of the different populations x_{ij} in relation to the total species population size (breeding population). Asterisks mark instances with a fluctuating migration pattern, for which average population sizes are presented.

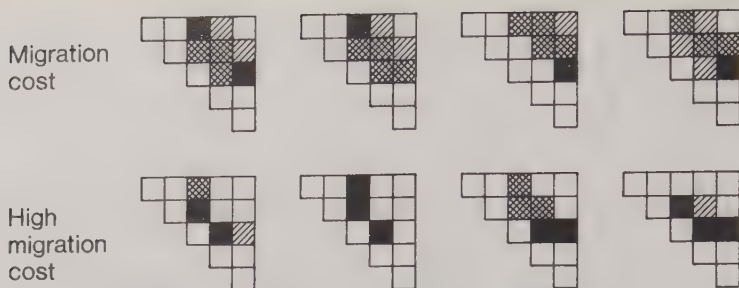


Figure 3. Stable migration patterns under different latitudinal breeding and wintering suitability conditions (the same column conditions as in Fig. 2) with migration costs ($d_1, d_2 > 0$). Asymmetric competition is excluded ($a, c = 0$). The calculations refer to the case with $K_s/K_b = 3$ (cf. Fig. 2). Results are presented for two levels of migration costs, the second twice as high as the former. Symbols are the same as in Fig. 2.

(B) Conditions for segregation.

Segregation occurs only when there is significant competition for breeding as well as winter survival resources. Hence, for $K_b \gg K_s$, i.e. in species with a great surplus of breeding resources in relation to survival resources (extreme B-species sensu Alerstam & Högstedt 1982), a migration pattern of the general type III in Fig. 1, with breeding confined to the most suitable latitude range, will be the result. Analogously, for $K_s \gg K_b$ (extreme S-species sensu Alerstam & Högstedt 1982), a migration pattern of type IV in Fig. 1, with wintering confined to the most suitable latitude range, will prevail.

Furthermore, when there are no significant migration costs (d_1 and $d_2 = 0$), segregation will occur only when there is asymmetric competition (either a or c , or both, > 0). However, even if there is asymmetric breeding competition, there will be no segregation unless there is a latitudinal gradient in breeding suitability. Similarly, with asymmetric winter competition, segregation will be associated with the existence of a latitudinal gradient in wintering suitability (Fig. 2).

(C) Leapfrog migration

The occurrence of distinct asymmetric competition for both breeding and wintering resources (a and $c > 0$) is a necessary but not sufficient condition for the development of leapfrog migration. As seen from Fig. 2, leapfrog migration occurs in two of the four instances illustrated for this condition with an approximate balance between wintering and breeding

resources (Case 1, $K_s/K_b = 1$, and in three of the four instances for a slightly more S-tinged species (Case 2, $K_s/K_b = 3$).

The leapfrog migration patterns are robust against the inclusion of migration costs. Such costs will not change the basic pattern, but merely lead to a truncation as the populations of long-distance migrants become reduced in size or eliminated.

(D) Chain migration

Chain migration will result when there is asymmetric competition either for breeding or wintering resources, provided there exists a latitudinal gradient in the corresponding breeding and wintering suitability. When there are distinct latitudinal gradients in both breeding and wintering suitability, a chain migration pattern is the consistent outcome with asymmetric competition for both breeding and wintering resources.

In addition, even without asymmetric competition, chain migration may develop as a consequence of migration costs (Fig. 3). It is somewhat paradoxical that migration costs lead to the elimination or reduction of resident populations in this way, but note that both p and q appear in the model in a fashion related to the influence of the competition factors (cf. equation 3).

(E) Latitudinal rates of reproduction and survival

We have, for the stable migration patterns, calculated the overall rates of reproduction and winter survival at the different latitudinal sites. When there is neither asymmetric competition nor migration costs, and consequently no segregation, there will be no latitudinal differences in those rates.

For the instances with no segregation in Fig. 2, asymmetric breeding competition has the effect of equalizing reproductive rate at different latitudinal sites, while winter survival increases towards the south. Conversely, asymmetric winter competition leads to equal winter survival over the latitudes, while reproduction increases towards the north.

For chain and leapfrog migration, the corresponding latitudinal patterns of reproduction and survival are more clearcut (Fig. 4). In all instances of chain migration in Figs 2 and 3, the overall reproductive rate consistently increases towards the north and the winter survival rate increases towards the south. In contrast, leap-frog migration is associated with either an increase in both reproduction and winter survival towards the north (in B-tinged species with a relatively high reproductive rate

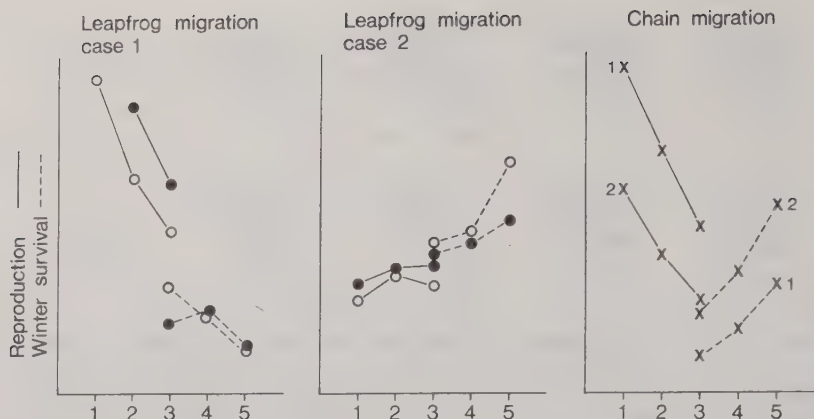


Figure 4. Overall rates of reproduction and winter survival at different latitudes (sites 1-5) with stable leapfrog and chain migration. Illustrated are examples with asymmetric competition for breeding as well as wintering resources, for leapfrog migration from the first and second columns in Fig. 2 (filled symbols denoting first-column conditions), and for chain migration from the third column in Fig. 2 (cases 1 and 2).

and low survival) or a decrease in these two rates towards the north (more S-tinted species). Of course, there must also be intermediate instances of leap-frog migration with minor and less consistent latitudinal trends in overall reproduction and survival rates (like the instance in the fourth column, case 2, in Fig. 2).

LONGITUDINAL SEGREGATION

We analysed longitudinal breeding segregation between two major wintering populations by a simulation model incorporating the effects of migration costs (proportional to the straight-line distance between breeding and wintering sites), asymmetric winter competition (disfavouring individuals from successively more distant breeding populations) and asymmetric breeding competition (disfavouring individuals from the most distant of the two wintering areas). Hence, birds with a short migration distance are assumed to have a competitive advantage, because presumably they can arrive relatively early to the breeding and wintering quarters.

Distinct longitudinal breeding segregation with a sharp migratory divide, occurs when there are significant migration costs and/or asymmetric winter competition (Fig. 5). With asymmetric breeding competition, such

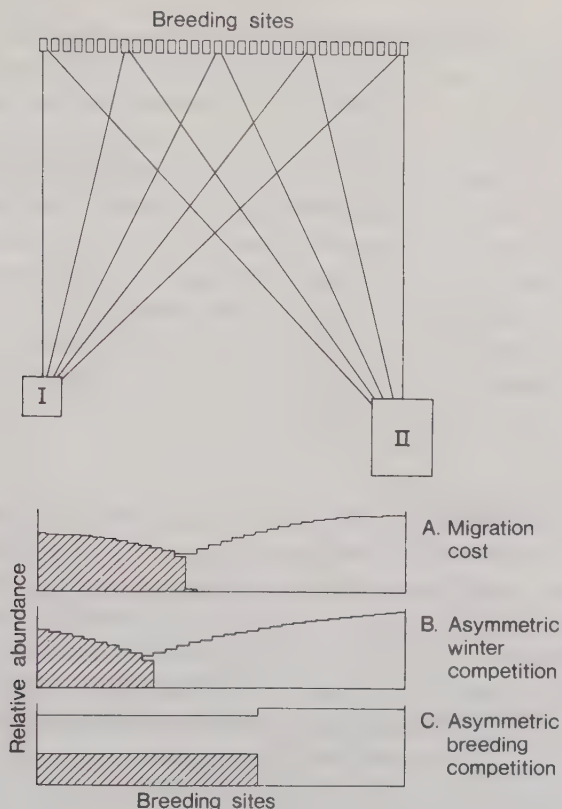


Figure 5. Relative abundance at different longitudinal breeding sites of individuals from two major wintering populations, I (hatched) and II. Stable patterns with migration costs (A), and with asymmetric competition for wintering (B) and breeding (C) resources, respectively, are shown in the lower three diagrams. The basic model is illustrated in the uppermost part of the figure: Two major wintering sites, one with three times as much resources for winter survival as the other, are situated at slightly different distances from the breeding latitude. We used a system with 32 longitudinal breeding sites. Computations were initiated with all possible migratory populations equal, and lasted 250 iterations. Migration distances were calculated along the straight lines between the different breeding and wintering sites.

segregation emerges only when winter carrying capacity (K_s) is similar for the two wintering areas, according to the approximate condition

$$\alpha^{-1} < K_{s,I} / K_{s,II} < \alpha$$

where α is the asymmetric competition coefficient for breeding resources. In other cases of asymmetric breeding competition (without migration costs and asymmetric winter competition), longitudinal overlap like that illustrated in Fig. 5, will be the result.

Increasing migration costs and/or asymmetrical winter competition, may lead to a gap between the breeding distributions of the two populations (cf. the reductions in breeding abundance towards the migratory divides, Fig. 5), to an increasing extent with a decreasing ratio of total resources for winter survival to total breeding resources.

Analogous results apply to the reverse case of longitudinal winter segregation between birds from two major breeding populations.

CONCLUSION

Asymmetric competition between early- and late-arriving individuals seems to be a potent selection force for the evolution of population segregation in migratory birds. Such competition can explain both leapfrog and chain migration, depending on whether it is in operation at both breeding and winter quarters or at only one of them, and depending on environmental conditions in the form of latitudinal differences in breeding and wintering suitability. Chain migration may develop also without asymmetric competition, as a consequence of migration costs. Furthermore, longitudinal segregation with sharp migratory divides may be the result of asymmetric competition and/or migration costs.

The migration pattern may be further affected by differences in migration costs between spring and autumn migration for different populations X_{ij} . Such differences may arise because of competition and resource renewal/depletion at resting places, and overlap between resources used for breeding and survival/migration. We have not incorporated these complex relationships into the analysis, but restricted ourselves to the simplified overall assumption that migration costs are proportional to migration distance.

Asymmetric competition and migration costs may act as selection forces not only for geographical population segregation, but also for differential migration between sex and age classes (cf. Myers 1981, Gauthreaux 1982, Ketterson & Nolan 1983), and for flight and resting strategies during the migratory journey. For these latter strategies, three main optimization criteria can be distinguished: (1) minimal risk (for predation, desorientation, drift etc); (2) minimal energy expenditure; (3) minimal

duration of the migratory journey. The first and second criterion are expected to be most important when migration costs are relatively high, whereas the third criterion should be associated with keen asymmetric competition at the destination.

Hence, the relative importance of asymmetric competition and migration costs may be assessed indirectly by comparing the migratory habits of birds (in terms of resting and flight behaviour) with the expected optimal habits for obtaining maximum migration range either per unit of energy expenditure or per unit of time. The flight speed minimizing transportation costs differs from that minimizing the total duration of the migratory journey. More specifically, the maximum range flight velocity on a given energy reserve, V_{mr} , is found by solving $dP(V)/dV = P(V)/V$, where $P(V)$ is the power curve for bird flight (cf. Pennycuick 1975). In comparison, the flight speed associated with a minimal total migration time to the breeding or wintering destination can be calculated by solving $dP(V)/dV = [P(V) + E]/V$, where E is the average rate of energy accumulation during the resting periods in between the successive migratory flights (cf. Alerstam in press, Norberg 1981).

Asymmetric competition can also be investigated directly by comparing performance between individuals arriving early and late, at breeding as well as wintering areas. The outcome of contests between territory owners and intruders in relation to ownership time, is revealing in this respect (cf. Krebs 1982).

Asymmetric competition is most likely in species exploiting defendable resources, often through territoriality. Hence leapfrog migration is predicted primarily in species with elements of both breeding and nonbreeding territoriality, and with a noticeable resource limitation during breeding as well as wintering. These conditions seem to be fulfilled at least for some of the most distinct leapfrog cases, which are found among waders with a visual, space-demanding foraging behaviour (Pienkowski et al. 1985).

Bird ringing has revealed many cases of distinct migratory divides, e.g. in the Palaearctic between birds from W and E African or from African and Asian winter quarters, and in the Nearctic between birds from New and Old World winter populations. The importance of asymmetric competition and migration costs for these migratory patterns, remains to be clarified.

The advantage of arriving early, in relation to competitors, at their seasonal living stations, may be of widespread importance to migratory birds. Much of the migrants' ways of existence, characterized by swiftness

and impatience, may derive from this selection force: to be, relative to others, an early bird.

REFERENCES

- Alerstam, T. in press. Strategies of migratory flight, illustrated by Arctic and Common Terns, *Sterna paradisaea* and *Sterna hirundo*. - Proc. Migration: Mechanisms and Adaptive Significance (The University of Texas at Austin).
- Alerstam, T. & Enckell, P.H. 1979. Unpredictable habitats and evolution of bird migration. - *Oikos* 33: 228-232.
- Alerstam, T. & Högstedt, G. 1980. Spring predictability and leapfrog migration. - *Ornis Scand.* 11: 196-200.
- 1982. Bird migration and reproduction in relation to habitats for survival and breeding. - *Ornis Scand.* 13: 25-37.
- 1985. Leap-frog arguments. Reply to Pienkowski, Evans and Townshend. - *Ornis Scand.* 16: 71-74.
- Gauthreaux, S.A. 1982. The ecology and evolution of avian migration systems. - *Avian Biology*. Vol. 6 (eds Farner, D.S., King, J.R. & Parkes, K.C. Academic Press, New York): 93-168.
- Haartman, L.v. 1968. The evolution of resident versus migratory habit in birds. Some considerations. - *Ornis Fennica* 45: 1-7.
- Ketterson, E.D. & Nolan, V. 1983. The evolution of differential bird migration. - *Current Ornithology* Vol. 1 (ed. Johnston, R. F. Plenum Publ., New York): 357-402.
- Krebs, J.R. 1982. Territorial defence in the Great Tit (*Parus major*): Do residents always win? - *Behav. Ecol. Sociobiol.* 11: 185-194.
- Myers, J.P. 1981. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. - *Can. J. Zool.* 59: 1527-1534.
- Nilsson, S. 1858. Skandinavisk Fauna. Foglarna. Första bandet. - Gleerups, Lund.
- Norberg, R.A. 1981. Optimal flight speed in birds when feeding young. - *Journ. Anim. Ecol.* 50: 473-477.
- Palmén, J.A. 1874. Om Foglarnes Flyttningsvägar. - Frenckell, Helsinki.
- Pennycuik, C.J. 1975. Mechanics of flight. - *Avian Biology*. Vol. 5 (eds Farner, D.S. & King, J.R. Academic Press, New York): 1-75.
- Pienkowski, M.W., Evans, P.R. & Townshend, D.J. 1985. Leap-frog and other migration patterns of waders: a critique of the Alerstam and Högstedt hypothesis, and some alternatives. - *Ornis Scand.* 16: 61-70.
- Salomonsen, F. 1955. The evolutionary significance of bird migration. - *Dan. Biol. Medd.* 22, No. 6, 62 pp.

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